PRIMARY PRODUCTIVITY BY PHYTOPLANKTON: TEMPORAL, SPATIAL AND TIDAL VARIABILITY IN TWO NORTH CAROLINA TIDAL CREEKS

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ABSTRACT

Tidal creeks along the Coastal Plain are subject to rapid increases in urbanization and the associated pollution can have profound effects on ecosystem processes. Temporal, spatial and tidal variability of one such process, phytoplankton primary productivity, was examined in two tidal creeks in southeastern North Carolina. Physical, chemical and biological data were used to assess the factors regulating phytoplankton productivity and the magnitude with which urbanization has affected ecosystem function within these systems. Annual phytoplankton productivity in un-canopied high tide waters was approximately 91 gC m^{-3} in Futch Creek and approximately 246 gC m^{-3} in Hewletts Creek. Elevated primary productivity corresponded with the summer chlorophyll *a* maxima in both creeks, but was significantly higher in the creek with greater watershed development, Hewletts Creek, during summer months. Spatial variability in primary productivity in Hewletts Creek indicated upper oligohaline to mesohaline reaches were characteristically more productive during summer months than lower euhaline creek areas. Although there were defined temporal trends in phytoplankton productivity in the lesser developed Futch Creek, spatial variability between creek reaches was not as pronounced. Primary productivity was generally higher at low tide when compared to high tide in both creeks. Decreased water column irradiance occurred periodically in the upper reaches of both creeks, especially following meteorological events. Nutrient concentrations in Hewletts Creek, especially ammonium and orthophosphate, were generally higher than in Futch Creek and were elevated at upstream sites and seasonally during summer months. Regression analyses indicated that 83% of the variability in phytoplankton primary production was explained by variations in temperature and phytoplankton biomass. The data suggest that the physical environmental forces of a dynamic tidal creek system govern basic seasonal, spatial and tidal patterns, but sediment and nutrient inputs from upland development could have a pronounced effect on the magnitude of a key ecosystem process, phytoplankton primary productivity. Comparative analysis indicates that volumetric phytoplankton productivity in local tidal creeks was on par or greater than other larger North Carolina estuaries. This suggests that tidal creeks should be valued as a coastal resource and management efforts should be implemented to preserve and possibly restore environmental integrity.

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DEDICATION

This research is dedicated to my parents who never cease to amaze me and have been my biggest cheerleaders in life. Thank you for making me a better individual and scientist. I would also like to dedicate this work to the family and friends who have stood behind me unconditionally in the pursuit of my scientific goals. I have been amazed by your unwavering support and motivation. Thank you all for being there when I needed you the most.

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INTRODUCTION

The structure of photosynthetic populations in freshwater, estuarine and marine systems is important to ecosystems ecology. Phytoplankton have a potential for substantial primary production and provide a nutritional base to estuarine food webs. Hence, the production of new organic matter by the phytoplankton community is a fundamental measure of the richness of aquatic ecosystems. Since phytoplankton primary production generates a flow of energy that moves up the estuarine food web and can eventually be harvested commercially, it is important to understand the dominant forces that control or alter this energy (Mallin and Paerl 1994).

Typically, marine and freshwater phytoplankton abundance is dependent on a number of physical environmental factors including, but not limited to, light, temperature, salinity and some function of nutrient availability. The photosynthetic capacity of phytoplankton is dependent on the vertical attenuation of light. This photosynthesis-irradiance relationship originates from light-dependent changes in photosynthesis over the course of a photoperiod and varies between light-limited, light-saturated, and photoinhibited rates (Behrenfeld et al. 2002). Phytoplankton abundance is also dependent on the availability of nutrients. According to Liebig's Law of the Minimum, "… growth of a plant is dependent on the amount of food stuff which is presented to it in minimum quantity" (Martin 1991). Nitrogen, phosphorus, and iron, among other nutrients, have been shown to limit algal growth in freshwater, coastal and open ocean systems (Martin 1991, Hecky and Kilham 1988, Ryther and Dunstan 1971). The biological characteristics of the system also play a role in regulating primary productivity, as phytoplankton abundance can be a function of grazing. Zooplankton community grazing rates have shown a positive correlation with primary productivity and phytoplankton abundance in the Neuse River Estuary (Mallin and Paerl 1994), and studies in the Chesapeake Bay demonstrate seasonal trends whereby zooplankton grazing of phytoplankton is greatly reduced due to top-down control by ctenophores and sea nettles (Baird and Ulanowicz 1989).

Biological activity including phytoplankton productivity and abundance has been shown to correspond to seasonal fluctuations in water temperature throughout many east coast estuaries (Caffrey 2004, Dame et al. 2000, Lewitus et al. 1998, Mallin 1994, Baird and Ulanowicz 1989). A literature review of estuarine phytoplankton by Mallin (1994) suggested that a geomorphological range of estuarine types along coastal North Carolina display underlying seasonal patterns whereby estuarine phytoplankton productivity and biomass generally rise and fall with water temperature and day length. Estuaries along the coast of South Carolina and Georgia often exhibit a chlorophyll *a* summer maximum with concentrations declining during late fall and winter as well as marked seasonal differences in the relative taxonomic contributions by microalgae (Dame et al. 2000, Lewitus et al. 1998). A comprehensive study of 22 National Estuarine Research Reserves along the U.S. east coast suggested that temperature is the most important environmental factor explaining variability in metabolic rates with peak production occurring during the summer in Southeastern estuaries (Caffrey 2004).

Estuaries are inherently dynamic systems, which can be subject to turbulent mixing by tide-, current- and wind-induced motions, altering environmental factors over short time scales (Hubertz and Cahoon 1999, Litaker et al. 1987). Field observations have revealed frontal zones in areas of freshwater and coastal water mixing characterized by sharp salinity changes, intense mixing, and color contrast (Dustan and Pinckney 1989). The variability in water clarity over a lunar tidal period is superimposed with the daily total irradiance and ultimately determines light exposure to phytoplankton. Suspended sediments and turbidity have been shown to change over the course of a tidal cycle in estuaries due to the advection of water masses of varying sediment load and resuspension of bottom sediments and microalgae during periods of high tidal flow (MacIntyre and Cullen 1996). In fact, the dynamic properties of shallow, turbid estuaries have led some researchers to believe that productivity in the water column might be dominated by resuspended benthic microalgae (MacIntyre and Cullen 1996). Vertical motions, however, cannot be generalized because the mixing regime has been shown to enhance, reduce and have no effect on primary production relative to static controls (MacIntyre and Geider 1996).

Tidal creek ecosystems are widespread and highly abundant along the Atlantic Seaboard and Gulf Coast. Unlike many larger neighboring estuaries, tidal creek systems do not necessarily follow a longitudinal river – ocean continuum and generally have a higher surface area to volume ratio than river-dominated estuaries. Collectively, this could make their importance in material transfer and other ecological processes on par or even greater than larger estuaries in some regions (Mallin and Lewitus 2004). Given all of this, there is still insufficient research published in the scientific literature concerning the metabolic processes within these tidal creek ecosystems.

Unfortunately, tidal creek ecosystems are enduring changes as a result of a steadily increasing human population along the Atlantic Coast, including southeastern North Carolina. Creeks that were once pristine are now urbanized, leading to a plethora of environmental concerns for adjacent watersheds. Urbanization results in disturbances such as land clearing, application of fertilizers, discharge of human and animal waste and increased impervious surface coverage, which collectively act to elevate elemental nitrogen and phosphorus concentrations in neighboring surface waters and ground waters (Cloern 2001). Nutrient over-enrichment, or eutrophication, can have profound effects on ecosystem processes by over-stimulating phytoplankton productivity and biomass accumulation leading to nuisance and toxic algal blooms (Cloern 2001). Eutrophication is also often associated with increased biochemical oxygen demand, hypoxia and anoxia (Mallin et al. 2005), reductions in available light energy for benthic plants and qualitative changes in the plant community, thus propagating changes in ecosystem trophodynamics (Cloern 2001). Trends show overall decreases in algal species diversity in streams with increasing urban land use usually due to factors including water chemistry (Paul and Meyer 2001).

Estuarine systems have a hydrological link to terrestrial landscapes and are thus subject to non-point source (NPS) runoff from the upland watershed. While locations near the mouth of an estuary would be expected to be more closely characteristic of the coastal ocean, headwaters can receive an influx of materials from the upland watershed. Chemical pollutants including nutrients, pesticides, and heavy metals bind to sediments from the terrestrial landscape and are introduced into water systems via NPS runoff. In an urban landscape nutrient molecules have been shown to travel further distances downstream before removal from the water column, suggesting nutrient removal efficiency can be greatly reduced by watershed urbanization (Paul and Meyer 2001). Urban streams in Atlanta have displayed a more negative net ecosystem metabolism (gross primary production – community respiration) when compared to forested streams (Paul and Meyer 2001). This increased heterotrophy was primarily attributed to increases in labile sources of carbon from the upland watershed (Paul and Meyer 2001).

Urbanization has also led to physical modifications of neighboring water systems. Alterations of the hydrology and geomorphology of streams can lead to changes in velocity profiles, sediment load and sediment size, all of which could affect mechanistic processes including carbon processing (Paul and Meyer 2001). Increased sediment loading alone can greatly reduce water column irradiance, which is problematic for photosynthetic processes. Also, bridges and culverts may serve as barriers to water flow and thus phytoplankton movement (Paul and Meyer 2001).

Problems associated with urbanization can be more pronounced in estuaries following rain events. A study by Mallin et al. (1993) demonstrated that the magnitude of primary production in the Neuse River Estuary could be directly correlated with upper watershed rainfall. During rain events, allochthonous sources of nitrogen are introduced to the upper basin via overland runoff and groundwater flow and lead to nutrient enrichment in the middle and lower basin and stimulation of productivity downstream. Freshwater runoff from the watershed has also been shown to exert a strong influence on the spatial and temporal distribution of phytoplankton in the Saint Lawrence Estuary whereby phytoplankton abundance can be physically restricted upstream due to high flushing (Therriault et al. 1990).

Two tidal creeks in southeastern North Carolina, Futch Creek and Hewletts Creek, were principal subjects of the current study. The New Hanover County Tidal Creeks Program has been monitoring Hewletts Creek monthly since late summer 1993. Futch Creek was added to the project in late summer 1994. Both creeks receive anthropogenic nutrient loading, especially in upstream areas, and have been host to occasional algal blooms (Table 1). The downstream portions of these creeks have shown sensitivity to nitrate-nitrogen inputs during bioassay experiments, indicating nitrogen limitation. Upper reaches have shown sensitivity to both nitrate-N and phosphorus. Occasionally the upper reaches of Hewletts Creek have had no response to nutrient enrichment

Table 1. Historical water quality trends in high tide surface waters in Hewletts Creek and Futch Creek from August 1999 – July 2003. Data presented as mean ± standard deviation/range.

Parameter	HC-2	NB-GLR	SB-PGR	FC-4	FC-6	FC-17
Temp (ºC)	20.0 ± 6.8 (6.8-30.9)	19.8 ± 7.2 (6.7-33.0)	19.8 ± 7.2 (6.4-32.0)	19.9 ± 6.8 (6.3-30.8)	19.9 ± 6.8 (6.1-30.7)	19.5 ± 6.7 (5.1-30.8)
DO (mg l^{-1})	7.4 ± 1.4 (5.3-10.9)	7.0 ± 2.6 (3.5-16.5)	6.9 ± 2.1 (3.5-11.4)	7.6 ± 1.9 (4.0-11.7)	7.6 ± 1.9 (3.8-11.8)	6.8 ± 2.5 (2.8-16.1)
Salinity	33.8 ± 2.3 (24.3-37.0)	12.1 ± 10.6 (0.8-32.7)	19.0 ± 9.4 (2.0-34.3)	33.7 ± 2.1 28.2-36.5)	32.7 ± 2.4 (25.7-36.5)	27.1 ± 7.7 (1.2-35.5)
Turbidity (NTU)	4 ± 2 (1-11)	12 ± 8 (2-37)	13 ± 7 (3-30)	6 ± 4 (1-19)	7 ± 3 (1-14)	14 ± 24 (2-164)
Ammonium-N $\mu g\ l^{-1}$	14.8 ± 14.0 (0.5-76.8)	45.7 ± 38.0 (1.4-190.1)	34.3 ± 29.1 (0.5-127.7)	21.6 ± 22.5 (0.0-138.9)	no data	36.5 ± 51.7 (0.0-288.4)
Nitrate-N $\mu g\ l^{-1}$	5.7 ± 5.8 (0.5-30.1)	92.7 ± 75.2 (0.5-257.7)	51.5 ± 63.9 (0.5-324.9)	7.1± 4.8 (0.8-19.8)	10.4 ± 8.3 (1.0-35.0)	74.9 ± 71.1 (2.7-272.2)
Orthophosphate $\mu g\ l^{-1}$	5.0 ± 3.1 (0.5-12.8)	16.0 ± 8.8 (6.1-49.5)	10.1 ± 5.8 (2.9-38.0)	6.3 ± 2.9 (1.0-13.8)	6.6 ± 3.0 (1.0-12.1)	11.9 ± 6.0 (0.0-25.0)
N:P Molar Raio	11.2 ± 9.0 (1.4 -42.2)	20.1 ± 12.1 (2.2-47.1)	19.9 ± 17.2 (2.2-102.6)	12.0 ± 9.4 (0.8-45.6)	no data	20.2 ± 13.9 (5.3-65.5)
Chl *a* $\mu g\ l^{-1}$	1.4 ± 0.8 (0.4-3.7)	12.3 ± 29.4 (0.8-165.7)	10.7 ± 12.9 (0.8-51.3)	1.3 ± 1.1 (0.2-4.9)	1.4 ± 1.2 (0.3-5.5)	6.3 ± 15.3 (0.5-106.1)

bioassays, suggesting that phytoplankton biomass may be light-limited, either through self-shading or elevated turbidity (Mallin et al. 2004).

Mallin et al. (1999a) conducted an earlier study of Hewletts Creek and Futch Creek and discovered that the phytoplankton community within these systems was very distinct. Phytoplankton biomass, measured as chlorophyll *a* concentration, was generally highest in upper Futch Creek during mid-tide and highest in upper Hewletts Creek during low tide. Total phytoplankton abundance was generally higher in Hewletts Creek at low tide and slightly higher in Futch Creek at high tide (Figure 1). During high tide in Futch Creek, the community was very diverse and high phytoplankton abundance was attributed to a greater number of tiny pennate diatoms (Mallin et al. 1999a). More flagellates characterized low tide in Futch Creek. Hewletts Creek phytoplankton abundances were more than an order of magnitude higher at low tide than high tide and the community was dominated by flagellates and cryptomonads (Mallin et al. 1999a; Figure 1).

The purpose of the current research is to provide a mechanistic study assessing the temporal, spatial and tidal variability of primary productivity by phytoplankton in shallow tidal ecosystems. Since both Futch Creek and Hewletts Creek are in varying stages of anthropogenic development it is a good opportunity to ascertain the primary forces governing phytoplankton primary productivity and abundance. The proposed hypotheses for this project are as follows:

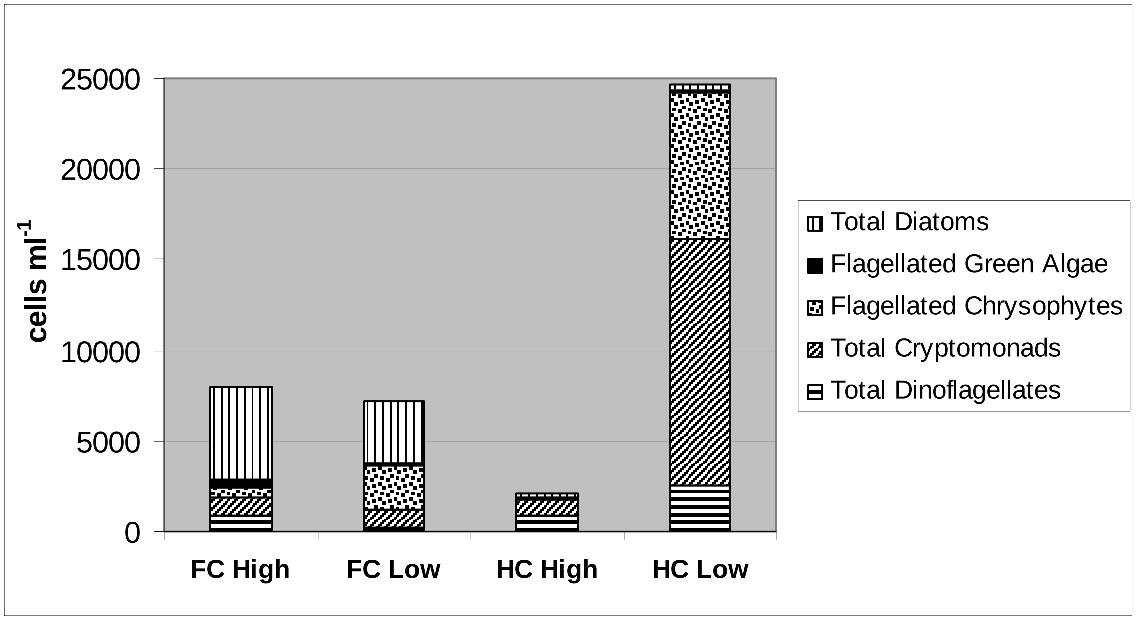


Figure 1. Phytoplankton abundance at high and low tide in upper reaches of Hewletts Creek (HC) and Futch Creek (FC), August 1996 (from Mallin et al. 1999).

H_1. Seasonally, primary productivity by phytoplankton will be highest during summer months in both Hewletts Creek and Futch Creek.

H_2. Spatially, primary productivity by phytoplankton will be higher in upper reaches of both creek systems when compared to downstream portions.

H_3. Tidally, primary productivity by phytoplankton will be higher during low tide in both creek systems.

H_4. Annual primary production by phytoplankton will be higher in Hewletts Creek than Futch Creek.

METHODS

Site Description

Two creeks located in Southeastern North Carolina were studied. The upper reaches of both creeks are characterized by muddy channels and oligohaline vegetation dominated by *Juncus roemerianus*. The lower creek consists of sandy sediments and scattered oyster reefs with salt marsh vegetation (mainly *Spartina alterniflora*) and flows into the U.S Atlantic Intracoastal Waterway. Futch Creek is a 2nd order tidal creek located at 34º 18'N latitude, 77º 55' W longitude, in Pender County, NC (Figure 2). In 1995 and 1996 the mouth of Futch Creek was dredged to improve creek circulation which resulted in a statistically significant increase in salinity in the months following dredging (Mallin et al. 2000). The Futch Creek watershed has comparatively lower development than that of adjacent tidal creeks with only approximately

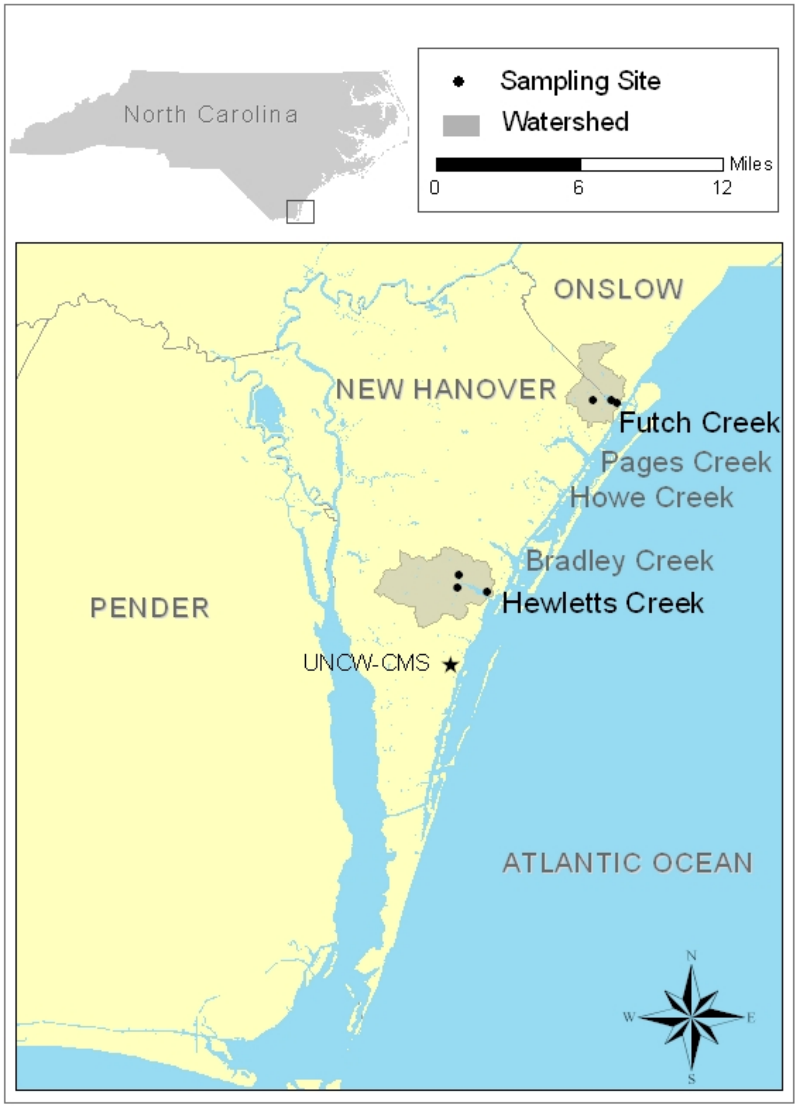


Figure 2. New Hanover County tidal creeks, coastal North Carolina, USA. (Map courtesy of H. Wells, 2005).

11% impervious surface coverage. Watershed development consists of residential properties and a golf course. Futch Creek also receives groundwater inputs of nitrogen in several locations by small natural springs (Roberts 2002). Hewletts Creek is a 3rd order tidal creek located at 34º 11'N latitude, 77º 50' W longitude, in New Hanover County, NC (Figure 2). Development within the Hewletts Creek watershed is on the rise with approximately 21% impervious surface coverage. Watershed development consists of a number of commercial and residential properties as well as two golf courses, all potential sources of non-point source runoff, especially in the upper reaches.

Tidal creeks within this region do not usually freeze during winter months and water temperatures can exceed 30ºC during summer months (Table 1). Tidal range in this area is around 1.1 m (Dame et al. 2000). A total of six sites were studied. There were three study sites within Futch Creek (FC-4, FC-6 and FC-17; Figure 3). Site FC-4 is a downstream site in the main channel of the creek. Average depth at FC-4 at high tide is approximately 2.0 m and depth at low tide averages approximately 1.0 m. Site FC-6 is located just downstream of the Foy branch tributary and is within the main channel of the creek. Average depth at FC-6 at high and low tide is 2.0 m and 1.0 m respectively. FC-17 is the site furthest upstream and is located in the upper south branch of Futch Creek. Natural springs feed into numerous areas of the south branch of Futch Creek including just upstream of site FC-17 (Roberts 2002). At high tide the average depth at FC-17 is approximately 1.2 m. At low tide the average depth is <0.2 m.

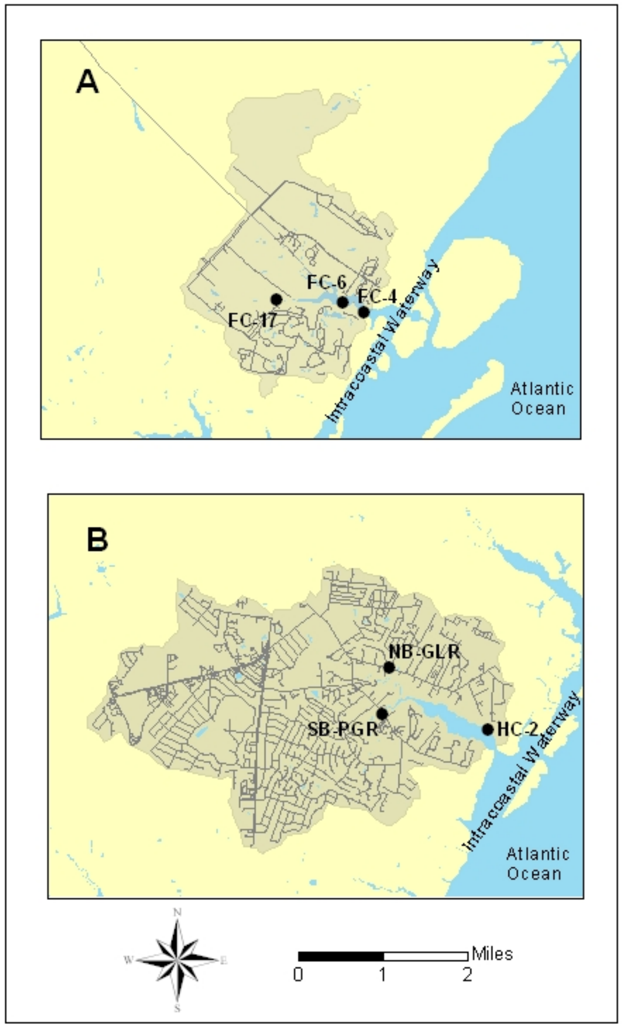


Figure 3. Futch Creek and Hewletts Creek watersheds. (Map courtesy of H. Wells, 2005).

Average salinities are euhaline at FC-4 and FC-6 and polyhaline at FC-17; however there has historically been a wide range of salinities at FC-17 (Table 1).

There were also three sites studied in Hewletts Creek (HC-2, NB-GLR and SB-PGR; Figure 3). HC-2 is a downstream site located in the main channel of the creek. The average depths at high and low tide are 2.0 m and 1.0 m, respectively. Site NB-GLR is located upstream in the north branch of Hewletts Creek. The average depth at high tide is approximately 1.0 m, and the average depth at low tide is <0.3 m. Site SB-PGR is located upstream in the south branch of Hewletts Creek. The average depth at high tide at SB-PGR is approximately 1.2 m and the average depth at low tide is approximately 0.8 m. Average salinities are euhaline at HC-2, polyhaline at SB-PGR, and mesohaline at NB-GLR (Table 1).

Field Sampling and Laboratory Methods

Field sampling was conducted monthly at high ebb tide from October 2003 thru September 2004. Beginning in March 2004 sampling was conducted monthly at both high ebb and low tide. During the month of July 2004 a time series sampling event occurred at high, mid, and low ebb tide. Study sites were chosen based on historical water quality data from the New Hanover County Tidal Creeks Program as well as accessibility at low tide.

Field parameters were measured using a YSI 6920 Multiparameter Water Quality Probe interfaced with a 650 MDS data logger. Vertical profiles of field parameters included water temperature, pH, dissolved oxygen, turbidity, salinity (PSU) and specific conductivity. Light attenuation was collected *in situ* using vertical profiles collected with a Li-Cor LI-193S spherical quantum sensor interfaced with a Li-Cor LI-1400 data logger. Secchi depth was also recorded. Total daily irradiance was logged at the UNCW Center for Marine Science, New Hanover County, NC, (Figure 2) during the week of sampling using a Li-Cor pyranometer interfaced with a Li-Cor LI-1400 data logger.

Rates of primary productivity by phytoplankton were measured using the rate of incorporation of radioactive carbon (^{14}C). The lower limit of sensitivity to the ^{14}C method is 0.01 mgC m^{-3} hr^{-1} and there is no theoretical upper limit to this method (Wetzel and Likens 2000). Vertical profiles of productivity were taken at surface and depth during high tide and only surface samples were collected at low tide due to depth restrictions. Samples were collected in 250 ml polystyrene cell culture flasks. Initial experiments were run in March of 2003 to test for significant differences between two methods of 'dark treatments' to account for non-photosynthetic uptake of radioactive carbon. Six samples were collected from site SB-PGR in Hewletts Creek. Three bottles were wrapped with aluminum foil to prevent the passage of light and three bottles were inoculated with 10.0μM DCMU (3-(3,4-dichlorophenyl)-1,1 dimethylurea), a photosynthetic electron transfer inhibitor. There was no significant difference found between the two methods. Therefore, due to tidal time constraints, the method of choice for this study was to use the photosynthetic inhibitor. Dark treatments were inoculated with 10.0μM DCMU. All samples were then inoculated with 2.0μCi $NaH^{14}CO_3$ and kept in the dark until ready for incubation. Duplicate light and single dark samples were incubated for 3 to 4 hours, centered around local noon. Given the potential for tidal and wind mixing in these systems, all samples were incubated *in situ* at equal surface depths. A Plexiglas bottle rack was equipped with floats to suspend bottles just below the surface of the water. At the end of incubation samples were kept in dark conditions until filtration. All samples were filtered individually and filters were placed into separate glass vials containing 10 ml of Fisher Scientific Scinti-Safe scintillation cocktail. Samples were radioassayed using a LKB Wallace 1214 Rackbeta Liquid Scintillation Counter. Total primary productivity was determined from the equations in Wetzel and Likens (2000). Primary productivity values were expanded into daily values based on total daily irradiance and then into expression on an annual basis with the aid of a CalComp Drawing Board III electronic digitizer and ArcView 3.0 computer software.

Phytoplankton biomass was estimated via chlorophyll *a* pigment analysis. Triplicate 125 ml amber bottles were filled ca. 10 cm below the surface and stored on ice until processing. Samples were filtered through Gelman A/E glass fiber filters (nominal pore size 1.0 micrometer). All filters were wrapped individually and frozen. Pooled filtrate was frozen for nitrate-nitrite (hereafter referred to as nitrate) and orthophosphate analysis. Chlorophyll *a* pigment concentration was analyzed using a fluorometric technique (Welshmeyer 1994). Phytoplankton samples were collected during spring and summer at low and high tide and field preserved with Lugol’s iodine. Dominant taxa were quantified using an Olympus BX50 phase contrast microscope.

Nitrate and orthophosphate was analyzed using a Bran-Leubbe AutoAnalyzer III following EPA protocols. Samples for ammonium were collected in duplicate, field preserved with phenol, and frozen until processed according to the methods of Parsons et al. (1984). Dissolved inorganic carbon (DIC) samples were taken in triplicate and field preserved with chloroform to decrease biological activity until processing. DIC (mgC l^{-1}) was analyzed using a Shimadzu TOC-5050A total organic carbon analyzer equipped with an NDIR detector (Shimadzu Aplication Note TOC-002).

Data Analysis

Statistical analyses were conducted using SAS statistical software (Schlotzhauer and Littell 1987). Initially, all variables were tested for normality using the Shapiro-Wilk test. Variables which were not normally distributed were log – transformed to achieve normality. Students *t*-tests were used to analyze for significant differences between surface and depth for each parameter ($p<0.05$). Analysis of variance was used to test for seasonal, spatial and tidal variability within and between creeks. Pair-wise correlation analysis was utilized to look for significant relationships between productivity, biomass and physical – chemical parameters ($p<0.05$). Since numerous variables co–varied in this data set, principal components analysis was utilized to determine relationships among productivity, biomass and physical – chemical parameters. Regression analysis was used to produce a predictive model of daily phytoplankton productivity.

RESULTS

All sites were sampled at high tide, however, only sites FC-4 and FC-6 in Futch Creek and sites HC-2 and SB-PGR in Hewletts Creek were sampled at low tide. Sites FC-17 in Futch Creek and NB-GLR in Hewletts Creek were only sampled twice at low tide during the winter of 2003 due to depth restrictions and therefore were not included for statistical analysis in this data set.

Physical – Chemical Parameters

Water temperatures in Futch and Hewletts Creeks were comparable (Tables 2 and 3). Water temperatures in Hewletts Creek ranged from 8.3ºC to 27.3ºC, with a mean of 19.0ºC (Figure 4). Water temperatures in Futch Creek ranged from 5.9ºC to 27.5ºC, with a mean of 18.3ºC (Figure 5). Both creeks displayed decreasing water temperatures during late fall and winter, with water temperatures rising during spring and summer (Figures 4 and 5). Minimum water temperatures were recorded in January 2004 in both creeks. Water temperatures peaked in Hewletts Creek in July 2004 and in Futch Creek in September 2004 (Figures 4 and 5).

Futch Creek had a significantly higher mean salinity (ANOVA, p=0.0039) than Hewletts Creek throughout the course of this study (Tables 2 and 3). Hewletts Creek had a wide range in salinity between sites, from oligohaline to euhaline (Table 3; Figure 4). Futch Creek did not display as much spatial variability in salinity and sites generally ranged from mesohaline to euhaline

Table 2. Water quality parameters during high ebb tide at surface and depth in Futch Creek, October 2003 – September 2004. Data presented as mean ± standard deviation, n=12.
*Indicates significantly different from downstream reaches ($p<0.05$).

Parameter	FC-4		FC-6		FC-17	
	Surface	Depth	Surface	Depth	Surface	Depth
Water Temp (ºC)	18.9 ± 7.8	18.0 ± 7.5	18.6 ± 7.7	17.9 ± 7.6	17.5 ± 6.9	NA
DO (mg l^{-1})	7.4 ± 2.2	7.7 ± 2.1	7.4 ± 2.4	7.7 ± 2.4	6.7 ± 3.0	NA
Salinity	31.4 ± 6.3	32.1 ± 4.0	30.1 ± 7.9	31.5 ± 3.8	15.9 ± 6.9*	NA
Turbidity (NTU)	5.0 ± 3.3	5.0 ± 4.2	6.0 ± 5.0	5.0 ± 3.8	10.0 ± 7.8*	NA
Light Attenuation k (m^{-1})	1.1 ± 0.9	NA	1.5 ± 1.6	NA	1.7 ± 1.1	NA
Ammonium-N ($\mu g\ l^{-1}$)	24.6 ± 25.7	NA	25.5 ± 25.0	NA	31.8 ± 29.5	NA
Nitrate-N ($\mu g\ l^{-1}$)	12.8 ± 12.5	19.1 ± 19.9	14.8 ± 11.9	12.4 ± 7.7	121.5 ± 69.2	NA
Orthophosphate-P ($\mu g\ l^{-1}$)	8.4 ± 4.4	11.7 ± 6.5	9.7 ± 5.1	10.6 ± 5.7	32.5 ± 54.4	NA
N:P Molar Ratio	9.0 ± 4.0	NA	8.1 ± 3.4	NA	19.2 ± 11.4	NA
Chl *a* ($\mu g\ l^{-1}$)	1.4 ± 1.0	1.3 ± 0.6	1.4 ± 1.0	1.2 ± 0.8	2.2 ± 1.5	NA
Productivity (mgC m^{-3} day^{-1})	242 ± 343	342 ± 488	248 ± 349	335 ± 533	260 ± 328	NA

Table 3. Water quality parameters during high ebb tide at surface and depth in Hewletts Creek, October 2003 – September 2004. Data presented as mean ± standard deviation, n=12.
*Indicates significantly different from downstream reaches ($p<0.05$).

Parameter	HC-2		SB-PGR		NB-GLR	
	Surface	Depth	Surface	Depth	Surface	Depth
Water Temp (ºC)	19.5 ± 6.9	18.8 ± 6.6	18.9 ± 6.8	18.1 ± 6.7	18.5 ± 5.9	NA
DO (mg l^{-1})	7.6 ± 2.2	8.0 ± 2.0	6.6 ± 2.8	8.0 ± 3.8	7.1 ± 2.5	NA
Salinity	32.3 ± 2.4	33.0 ± 1.7	12.5 ± 5.5*	15.1 ± 5.2	5.0 ± 4.5*	NA
Turbidity (NTU)	4.0 ± 2.8	5.0 ± 2.2	9.0 ± 4.2*	10.0 ± 4.4	10 ± 6.4*	NA
Light Attenuation k (m^{-1})	0.9 ± 0.26	NA	2.5 ± 1.2*	NA	2.5 ± 1.6*	NA
Ammonium-N (μg l^{-1})	13.8 ± 9.5	NA	145.0 ± 366.0	NA	34.6 ± 27.9	NA
Nitrate-N (μg l^{-1})	8.2 ± 4.8	14.6 ± 9.9	69.4 ± 40.3*	47.7 ± 19.4	126.7 ± 37.3*	NA
Orthophosphate-P (μg l^{-1})	7.6 ± 4.1	9.9 ± 6.4	28.8 ± 35.2	18.8 ± 17.2	33.5 ± 30.4	NA
N:P Molar Ratio	0.5 ± 0.4	NA	16.4 ± 8.2	NA	15.9 ± 8.8	NA
Chl *a* (μg l^{-1})	1.3 ± 0.6	1.1 ± 0.5	4.8 ± 4.0*	3.5 ± 1.3	11.3 ± 18.5*	NA
Productivity (mgC m^{-3} day^{-1})	216 ± 224	256 ± 299	463 ± 415	352 ± 238	1,348 ± 2,399	NA

Figure 4. Seasonal and spatial trends in physical parameters in Hewletts Creek, October 2003 – September 2004, high tide surface waters. Shaded area represents growing season.

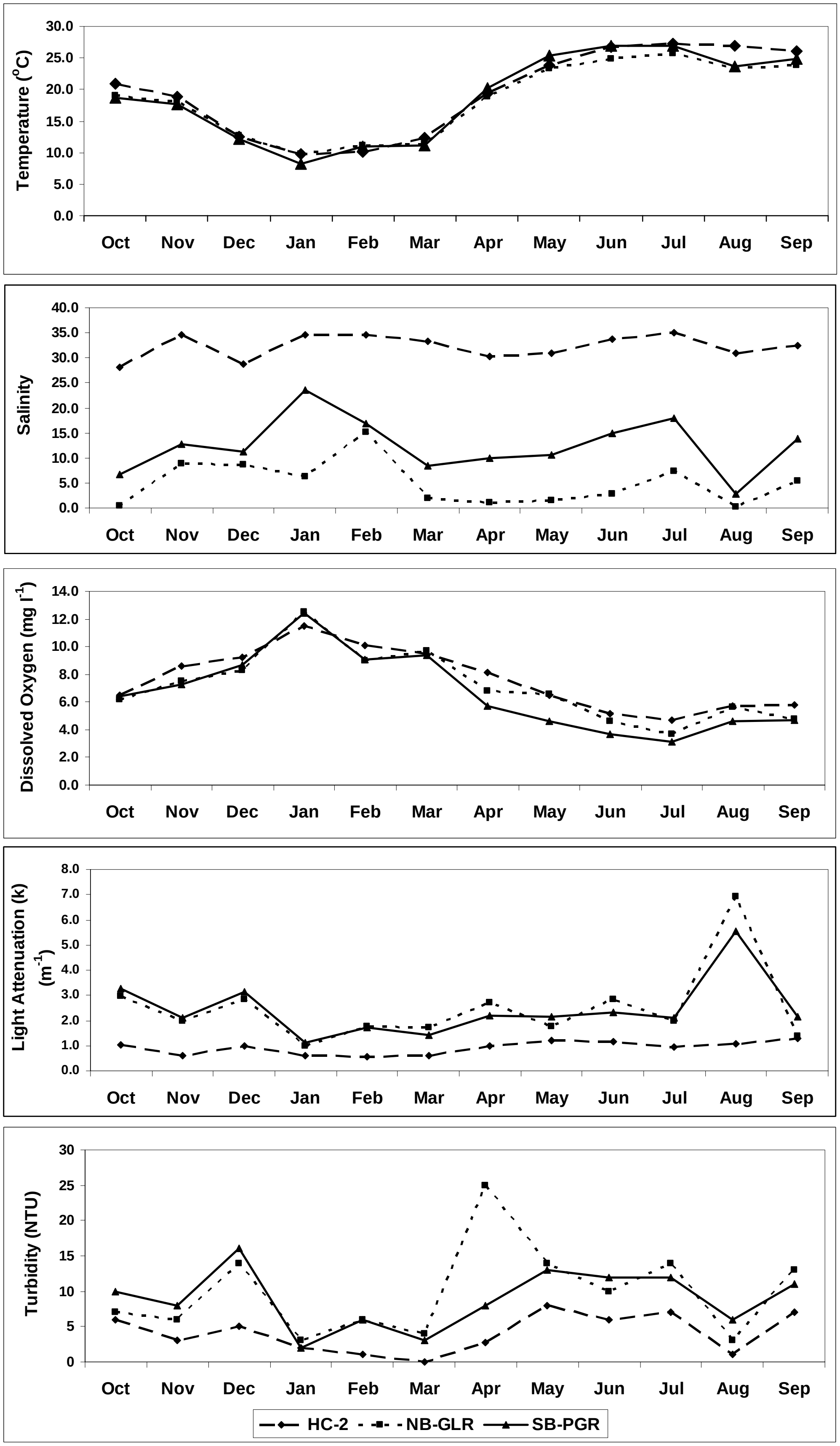
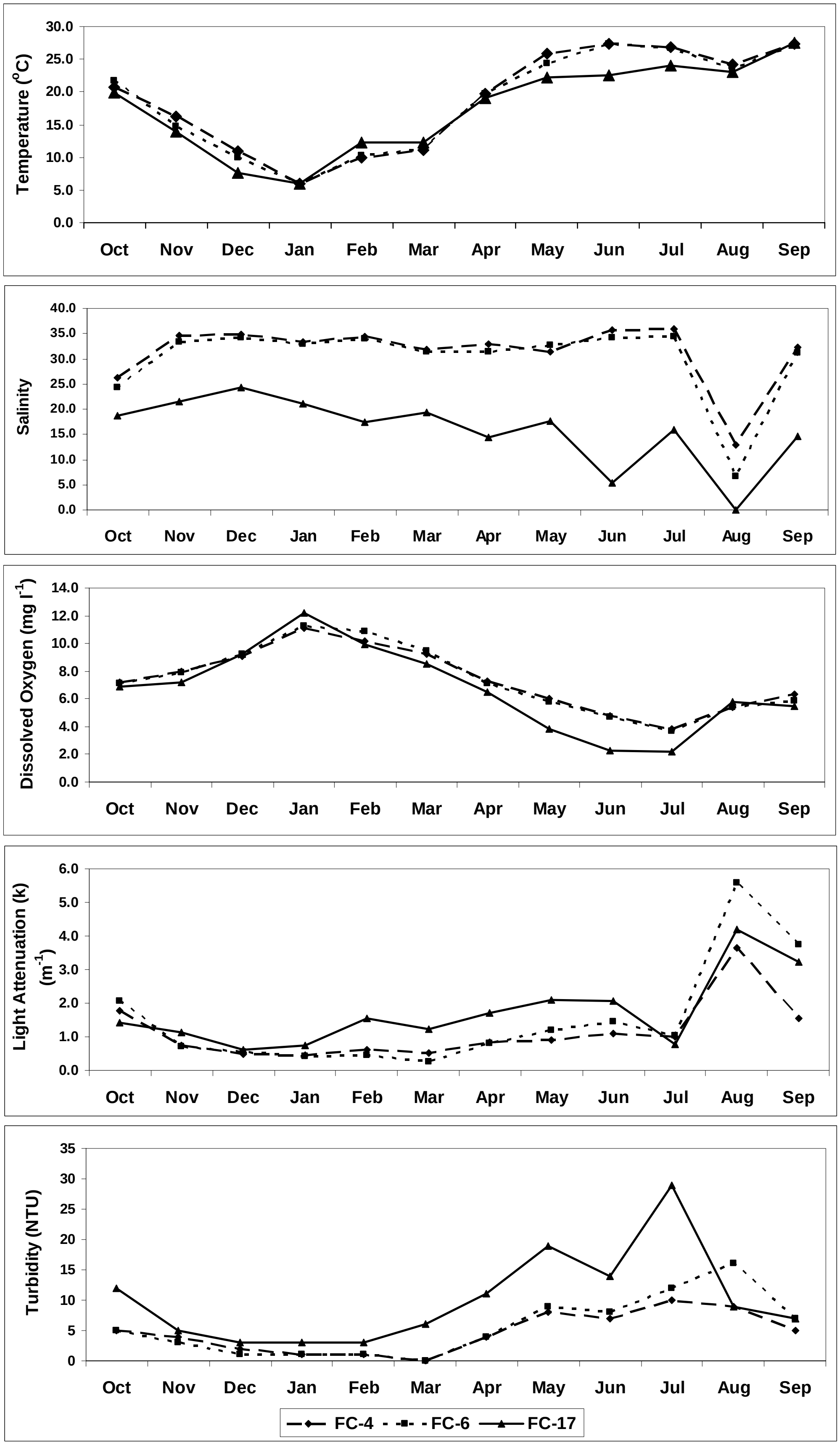

Temperature (°C)
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Salinity
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Dissolved Oxygen (mg l-1)
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Light Attenuation (k) (m-1)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Turbidity (NTU)
30
25
20
15
10
5
0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
HC-2
NB-GLR
SB-PGR

Figure 5. Seasonal and spatial trends in physical parameters in Futch Creek, October 2003 – September 2004, high tide surface waters. Shaded area represents growing season.



Temperature (°C)
Salinity
Dissolved Oxygen (mg l-1)
Light Attenuation (k) (m-1)
Turbidity (NTU)
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
FC-4
FC-6
FC-17

(Table 2, Figure 5). It should be noted that there was a drop in salinity, especially in Futch Creek, directly following Hurricane Charley in August 2004. The water column salinity tended to be well mixed; vertical profiles of mean salinity at surface and depth were not significantly different (t-test, Futch Creek p=0.7705, Hewletts Creek p=0.3952; Tables 2 and 3). Low tide mean salinity was on average 5-8% lower at low tide than high tide in both creek systems, however, there was no statistical difference (Tables 2, 3, 4, and 5).

Mean high tide surface dissolved oxygen (DO) concentrations were highest at study site HC-2 (mean= 7.6 mg l^{-1}) and lowest at site SB-PGR (mean = 6.6 mg l^{-1}) (Table 3). Both Hewletts Creek and Futch Creek had a mean surface DO concentration of 7.1 mg l^{-1} (Tables 2 and 3). Mean DO concentrations at depth were generally more elevated than surface concentrations; however this difference was not significant (t-test, Futch p=0.7113, Hewletts p=0.6971; Tables 2 and 3). For both creeks, DO concentrations were significantly higher (ANOVA, p<0.0001) during the winter months and began to decline during spring (Figures 4 and 5). Low tide DO concentrations were generally lower than concentrations recorded at high tide; however, this was not significant (ANOVA, p=0.0639; Tables 2 - 5). There were no incidents of hypoxia (defined as <2.0 mg l^{-1}) in surface or bottom waters at high tide during the sampling year, however, there was one incidence of hypoxia at site SB-PGR at low tide in August 2004 (1.3 mg l^{-1}; Figure 5; Table 5). It should be noted that in addition to Hurricane Charley, a spill of over 100,000 gallons of raw sewage occurred in Hewletts Creek at site SB-PGR in the month of August 2004, preceding the measured hypoxia.

Table 4. Water quality parameters during low tide in Futch Creek surface waters, March – September 2004. Data presented as mean $\pm$ standard deviation, n=7. *****Indicates significantly different from site mean high tide values ($p<0.01$).

Parameter	FC-4	FC-6
Temp (ºC)	24.1 $\pm$ 4.4	24.5 $\pm$ 4.3
DO (mg l^{-1})	5.2 $\pm$ 1.0	5.5 $\pm$ 1.3
Salinity	24.6 $\pm$ 11.6	22.4 $\pm$ 1.4
Turbidity (NTU)	18.0 $\pm$ 26.8	24.0 $\pm$ 37.0
Ammonium-N ($\mu g\ l^{-1}$)	46.4 $\pm$ 37.9	41.7 $\pm$ 40.7
Nitrate-N ($\mu g\ l^{-1}$)	44.7 $\pm$ 47.0	52.3 $\pm$ 34.4*
Orthophosphate-P ($\mu g\ l^{-1}$)	14.2 $\pm$ 9.3	15.7 $\pm$ 12.2
Chl *a* ($\mu g\ l^{-1}$)	3.0 $\pm$ 1.6	7.4 $\pm$ 7.6*
Productivity (mgC m^{-3} day^{-1})	619 $\pm$ 457	1,699 $\pm$ 2,196*

Table 5. Water quality parameters during low tide in Hewletts Creek surface waters, March – September 2004. Data presented as mean ± standard deviation, n=7. *****Indicates significantly different from site mean high tide values ($p<0.01$).

Parameter	HC-2	SB-PGR
Temp (ºC)	24.1 ± 5.1	23.3 ± 5.4
DO (mg l^{-1})	5.7 ± 1.0	5.5 ± 2.9
Salinity	24.0 ± 10.5	8.0 ± 6.1
Turbidity (NTU)	12.0 ± 11.1	18.0 ± 9.2
Ammonium-N ($\mu g\ l^{-1}$)	35.7 ± 34.9	259.3 ± 568.3
Nitrate-N ($\mu g\ l^{-1}$)	24.0 ± 26.7	31.0 ± 32.5*
Orthophosphate-P ($\mu g\ l^{-1}$)	14.8 ± 8.7	34.9 ± 45.9
Chl *a* ($\mu g\ l^{-1}$)	3.8 ± 1.2*	32.5 ± 22.7*
Productivity (mgC m^{-3} day^{-1})	924 ± 478*	3,433 ± 3,201*

Mean turbidity was comparable in Futch Creek (7 NTU) and Hewletts Creek (8 NTU) (Tables 2 and 3; Figures 4 and 5). The highest turbidity was at sites NB-GLR and FC-17 (mean = 10 NTU). Mean turbidity was significantly higher in the upper reaches of both creeks (ANOVA, p=0.0152; Figures 4 and 5). There was little variability in turbidity measured at the surface and at depth at all sites (t-test, Futch p=0.8407, Hewletts p=0.4955; Tables 2 and 3). Turbidity was also higher during summer months than winter months in both creeks (ANOVA, p<0.0001; Figures 4 and 5). Mean low tide turbidity was generally higher than high tide turbidity in both Futch and Hewletts Creek (ANOVA, p=0.0108), which was most likely attributed to resuspension of the sediment during low tide when water depths were less than 1.0 m (Tables 2 - 5). Light attenuation was only measured at high tide due to depth restrictions and accessibility and was greater in Hewletts Creek (Tables 2 and 3). Light attenuation was higher during summer months in Futch Creek (ANOVA, p=0.0003), however, there were no seasonal trends in Hewletts Creek (Figures 4 and 5). Much like turbidity, light attenuation was higher (ANOVA, p=0.005) in the upper reaches of Hewletts Creek, however, there was no significant spatial variability in Futch Creek (Tables 2 and 3). Peak light attenuation was recorded in August 2004, following Hurricane Charley.

General nutrient trends indicated higher concentrations in the upstream portions of both creeks (Figures 6 and 7). Nutrient concentrations were elevated in Hewletts Creek, especially at site SB-PGR (ammonium -N = 1,303 $\mu g\ l^{-1}$; nitrate -N = 135 $\mu g\ l^{-1}$; orthophosphate -P = 127.4 $\mu g\ l^{-1}$), during the sewage spill in August 2004 (Figure 6). Mean ammonium concentrations were higher in

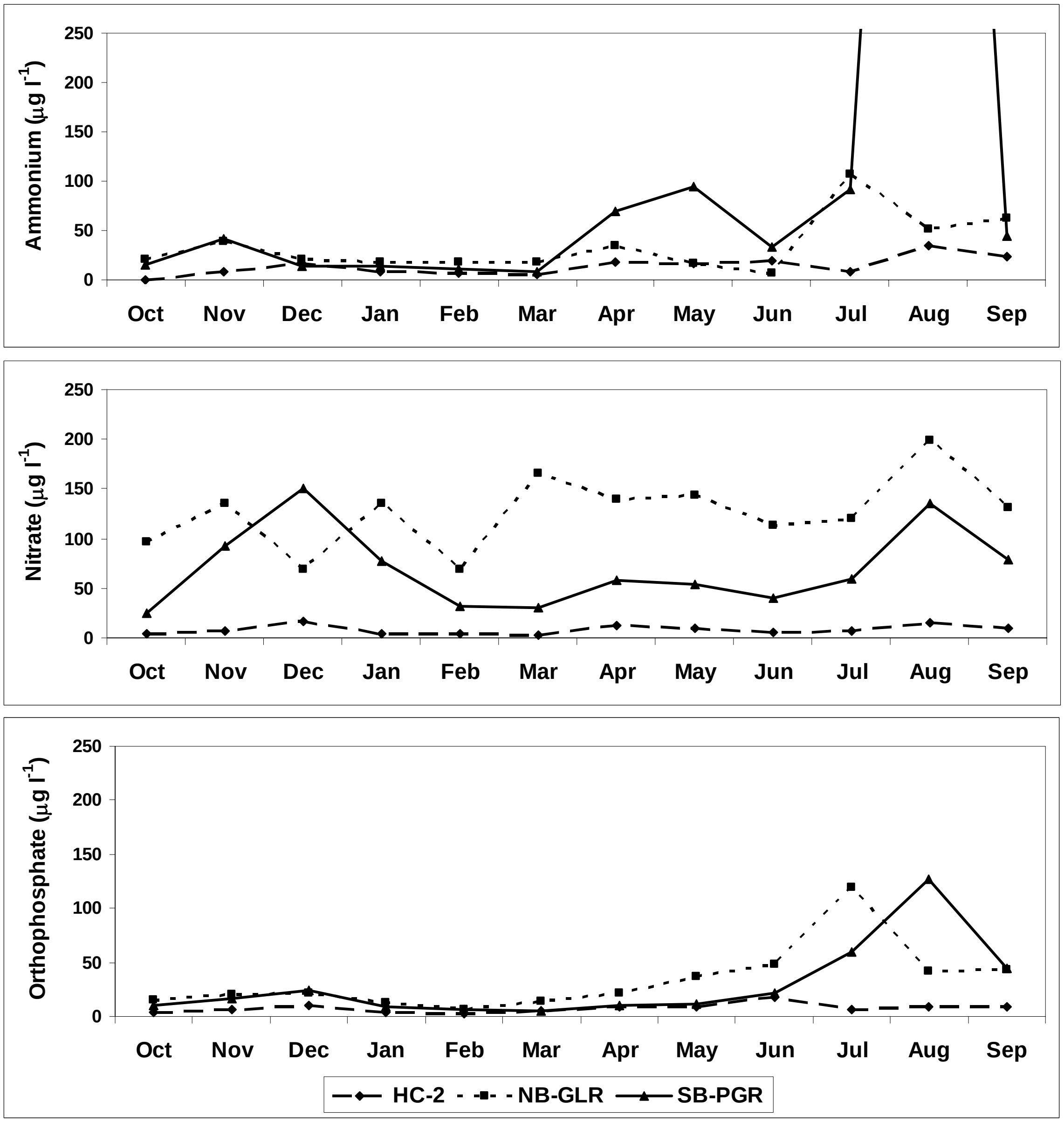


Figure 6. Seasonal and spatial trends in nutrient concentrations in Hewletts Creek, October 2003 – September 2004, high tide surface waters. Shaded area represents growing season.

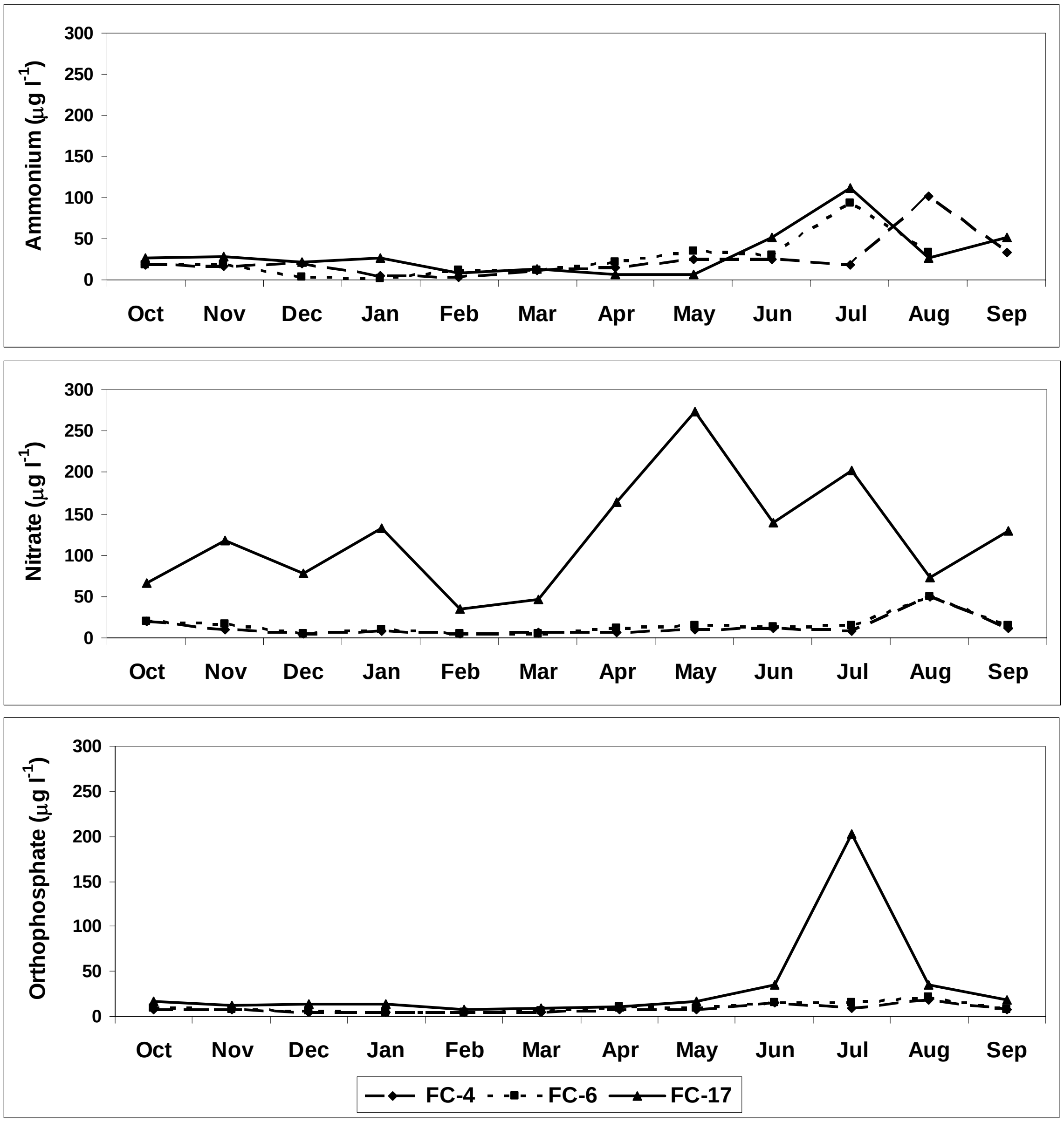


Figure 7. Seasonal and spatial trends in nutrient concentrations in Futch Creek, October 2003 – September 2004, high tide surface waters. Shaded area represents growing season.

Hewletts Creek (64.4 $\mu g\ l^{-1}$) than Futch Creek (27.3 $\mu g\ l^{-1}$), however, this was not a significant difference (ANOVA, p=0.4320; Tables 2 and 3). Ammonium samples taken at high tide were the most elevated at site SB-PGR (mean = 145.0 $\mu g\ l^{-1}$) and lowest at site HC-2 (mean = 13.8 $\mu g\ l^{-1}$;Table 3). Mean ammonium concentrations at low tide were also highest at site SB-PGR (mean = 259 $\mu g\ l^{-1}$) and lowest at site HC-2 (mean = 35 $\mu g\ l^{-1}$;Table 5, Figure 6). Ammonium concentrations were higher during summer months in both Futch and Hewletts Creek (ANOVA, p=0.0001; Figures 6 and 7). Low tide ammonium concentrations were not significantly different from high tide in either creek (ANOVA, p=0.4109; Tables 2-5).

Nitrate concentrations were higher in Hewletts Creek (mean = 68.1 $\mu g\ l^{-1}$) than Futch Creek (mean = 49.7 $\mu g\ l^{-1}$) at high tide (ANOVA, p<0.0001) and nitrate concentrations were higher in the upper reaches of Hewletts Creek when compared to lower creek reaches (Tables 2 and 3; Figures 6 and 7). Nitrate concentrations at low tide were higher than high tide at all sites sampled (ANOVA, p<0.0001; Tables 2 -5). Average orthophosphate concentrations were also higher at high tide in Hewletts Creek (mean = 23.3 $\mu g\ l^{-1}$) than Futch Creek (mean = 16.9 $\mu g\ l^{-1}$), however this difference was not significant (ANOVA, p=0.3174; Tables 2 and 3). Orthophosphate concentrations were higher during summer months (ANOVA, p<0.0001), and there were no significant differences in orthophosphate concentrations at low tide compared to high tide (ANOVA, p=0.3174; Figures 6 and 7; Tables 2 -5). Peak orthophosphate concentrations in Hewletts Creek occurred during August 2004 (Figure 6).

Phytoplankton Production and Biomass

Mean annual phytoplankton production during high tide was approximately 246 gC m^{-3} in Hewletts Creek and 91 gC m^{-3} in Futch Creek (Table 6). Mean daily productivity in Hewletts Creek was nearly double that of Futch Creek (Tables 2 and 3). There was apparent spatial variability between sites in Hewletts Creek, however, this was only significant during the summer months when primary productivity was higher at upstream site NB-GLR compared to downstream site HC-2 ($p=0.0006$; Table 3, Figure 8). There was no significant spatial variability in Futch Creek (ANOVA, $p=0.4270$; Table 2, Figure 9). The site with the highest mean daily productivity at high tide was site NB-GLR (mean = 1,348 mgC m^{-3} day^{-1}; Table 3). The site with the lowest mean daily productivity at high tide was site HC-2 (mean = 216 mgC m^{-3} day^{-1}; Table 3). Peak low tide productivity was at SB-PGR (mean = 3,433 mgC m^{-3} day^{-1}; Table 5). FC-4 displayed the lowest low tide productivity (mean = 619 mgC m^{-3} day^{-1}; Table 4). Water column productivity tended to be well mixed; there were no significant differences in vertical profiles of mean productivity in surface waters versus depth (t-test, Futch $p=0.7494$, Hewletts $p=0.9541$; Tables 2 and 3). Productivity was significantly higher at low tide in both creek systems (ANOVA, $p<0.0001$; Tables 2 – 5). Temporally, productivity was highest during late spring and summer and low during winter months (Figures 8 – 10). There was a decrease in high tide phytoplankton productivity directly following Hurricane Charley in August of 2004, when productivity would usually be elevated (Figures 8 and 9).

Table 6. Annual phytoplankton production in Futch Creek and Hewletts Creek, high tide. n=12.

Location	Volumetric gC m^{-3}	Areal gC m^{-2}
Futch Creek		
FC-4	88.3	97.2
FC-6	90.5	108.6
FC-17	94.9	71.2
Hewletts Creek		
HC-2	78.8	106.4
NB-GLR	492.0	295.2
SB-PGR	169.0	190.2

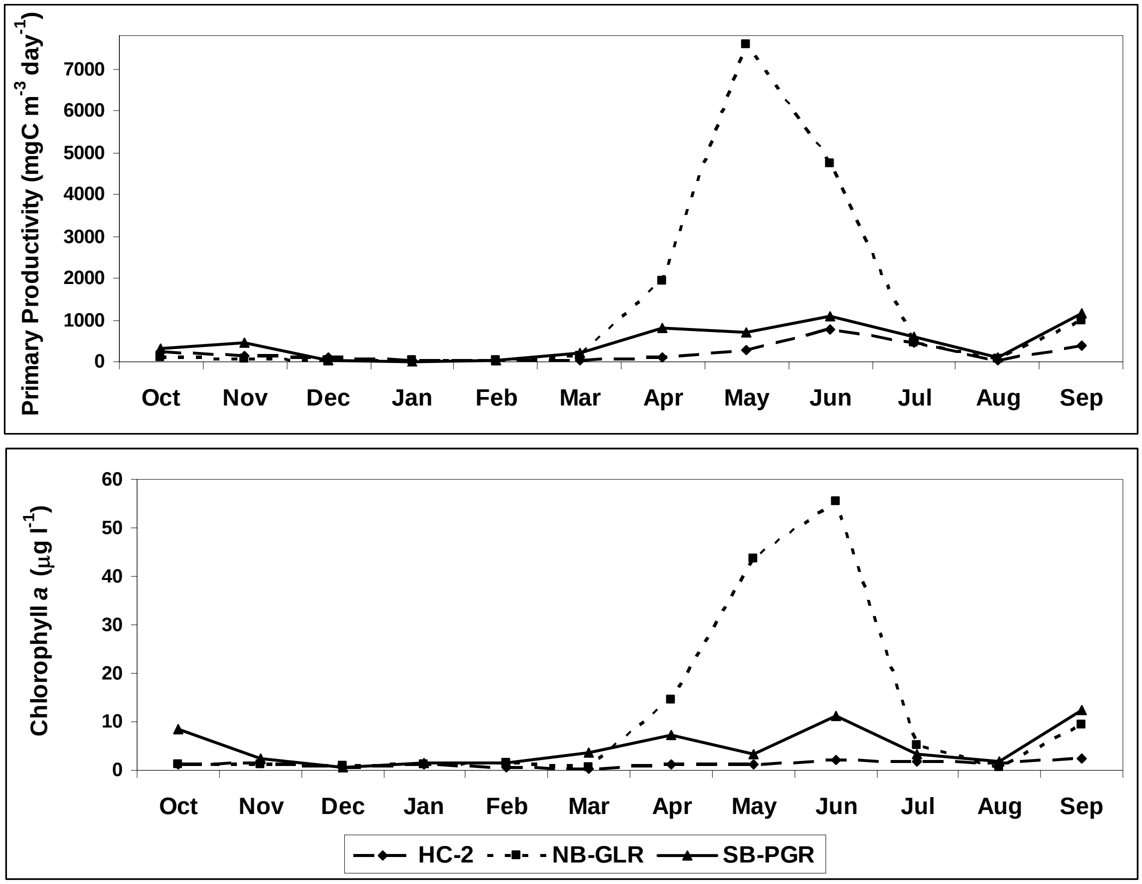


Figure 8. Seasonal and spatial trends in phytoplankton productivity and biomass in Hewletts Creek, October 2003 – September 2004, high tide surface waters. Shaded areas represents growing season.

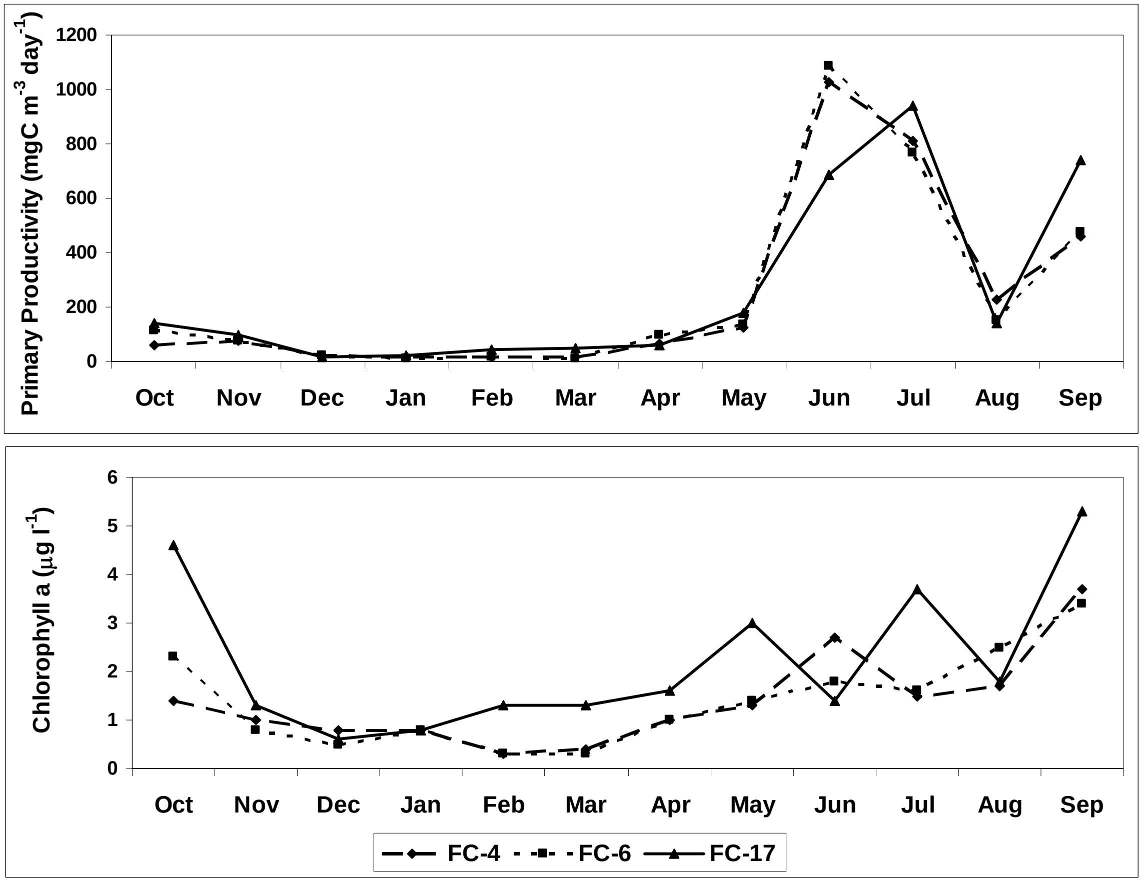


Figure 9. Seasonal and spatial trends in phytoplankton productivity and biomass in Futch Creek, October 2003 – September 2004, high tide surface waters. Shaded areas represents growing season.

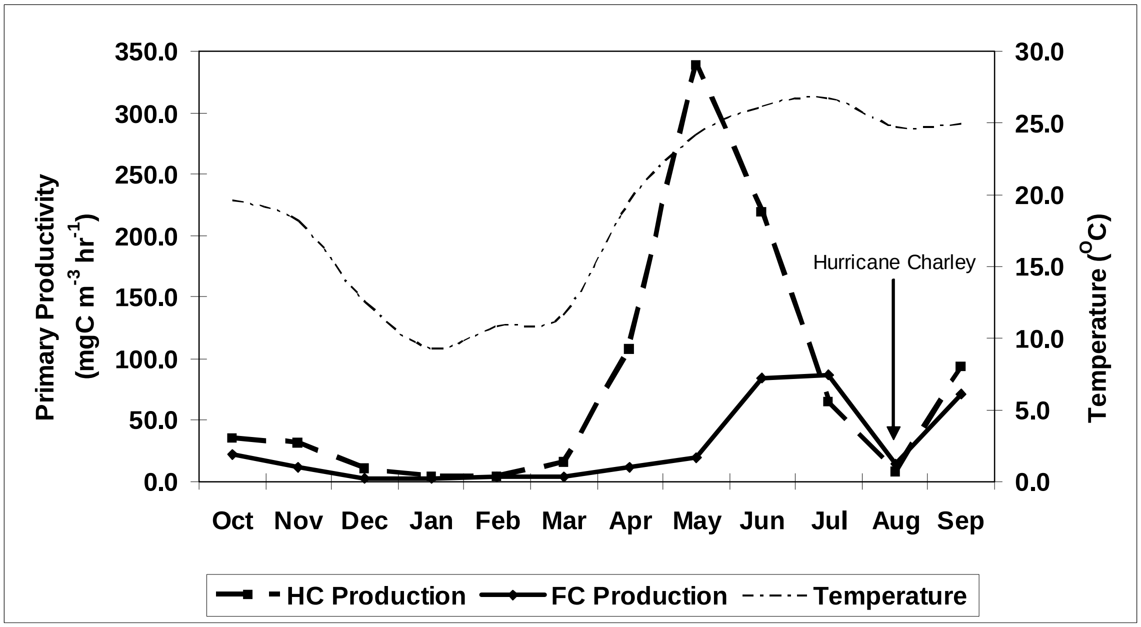


Figure 10. Primary productivity as a function of temperature in Hewletts Creek (HC) and Futch Creek (FC) in high tide surface waters, October 2003 – September 2004.

Mean chlorophyll *a* concentration was three times higher in Hewletts Creek (5.8 μg l^{-1}) than Futch Creek (1.7 μg l^{-1}; Tables 2 and 3). The highest mean chl *a* concentration at high tide occurred at site NB-GLR where algal blooms (defined as >25 μg l^{-1} of chl *a*) occurred in May and June of 2004 (Figure 8). Chlorophyll *a* concentrations were highest during summer months compared to winter months in both Futch and Hewletts Creek (ANOVA, $p<0.0001$; Figures 8 and 9). Mean chlorophyll *a* concentrations were also higher at low tide when compared to high tide in both creeks (ANOVA, $p<0.0001$; Tables 2 – 5). Algal blooms were also present at site SB-PGR at low tide during the months of April, May and June of 2004. Peaks in productivity coincided with the summer chlorophyll *a* maxima (Figure 11).

Assimilation rates, as carbon:chlorophyll *a* ratios, were calculated for all sites at high tide. Mean high tide assimilation rates were approximately 14 mgC (mg chl*a*)$^{-1}$ hr^{-1} in both Futch and Hewletts Creek. Assimilation rates in the upper reaches of Hewletts Creek were generally lower than lower reaches. Site NB-GLR yearly assimilation rates averaged 11.7 mgC (mg chl*a*)$^{-1}$ hr^{-1} (range, 2.4-25.6 mgC (mg chl*a*)$^{-1}$ hr^{-1}) and site SB-PGR yearly rates averaged 11.1 mgC (mg chl*a*)$^{-1}$ hr^{-1} (range, 1.7-27.5 mgC (mg chl*a*)$^{-1}$ hr^{-1}). The lower reaches of Hewletts Creek displayed higher assimilation rates averaging 19.7 mgC (mg chl*a*)$^{-1}$ hr^{-1} (range, 4.3-52.3 mgC (mg chl*a*)$^{-1}$ hr^{-1}). Yearly rates in Futch Creek averaged 16 mgC (mg chl*a*)$^{-1}$ hr^{-1} (range, 2.3-53.1 mgC (mg chl*a*)$^{-1}$ hr^{-1}) in the upper reaches and 12.3 mgC (mg chl*a*)$^{-1}$ hr^{-1} (range, 2.4-25.6 mgC (mg chl*a*)$^{-1}$ hr^{-1} in the lower reaches. Assimilation rates were highest during summer months and declined

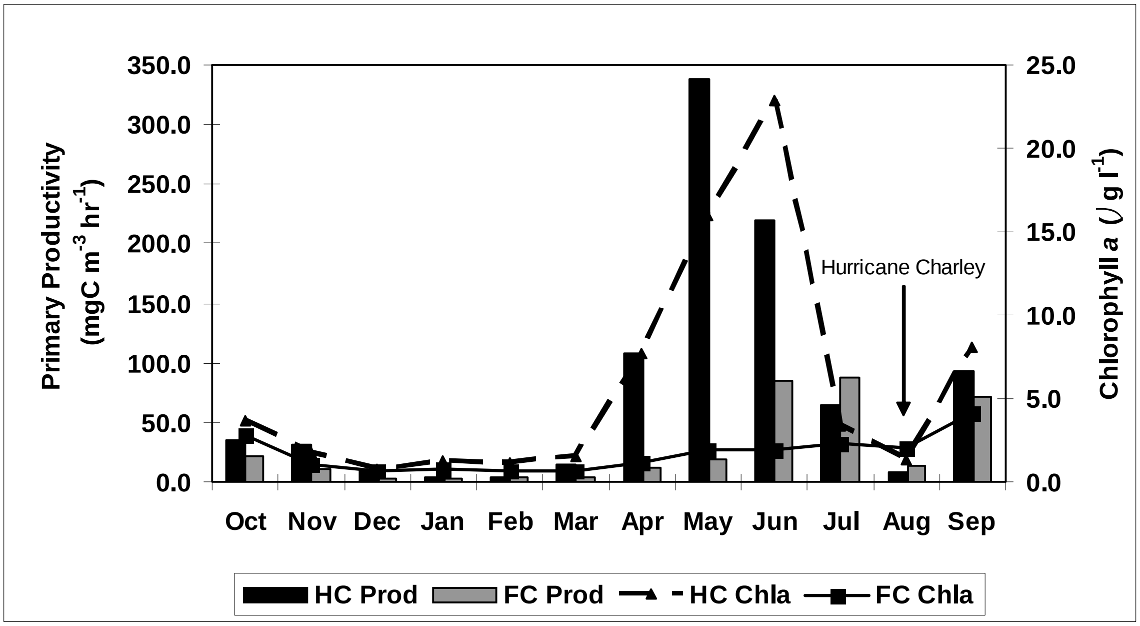


Figure 11. Primary productivity as a function of phytoplankton biomass in Hewletts Creek (HC) and Futch Creek (FC) in high tide surface waters, October 2003 – September 2004.

during winter and directly following Hurricane Charley. The assimilation rate during the sewage spill at site SB-PGR was approximately 5.0 mgC (mg chl*a*)$^{-1}$ hr^{-1}. Low tide rates ranged from 5.0 to 40.5 mgC (mg chl*a*)$^{-1}$ hr^{-1} in Hewletts Creek and 6.0 to 36.8 mgC (mg chl*a*)$^{-1}$ hr^{-1} in Futch Creek. Since low tide sampling was skewed towards summer months, seasonal trends will not be discussed.

Phytoplankton Assemblages

Periodic phytoplankton samples were collected and analyzed during the spring and summer of 2004. The lower reaches of Hewletts Creek were dominated by diatoms, especially *Navicula* spp. and *Nitzchia longissima*, and dinoflagellates especially *Gymnodinium* spp., at both high and low tide in late spring. Oligohaline reaches of Hewletts Creek were dominated by the cryptomonads, especially *Chroomonas amphioxeia* as well as dinoflagellates, predominately, *Gymnodinium* spp. in late spring. The mesohaline reaches of Hewletts Creek were characterized by chrysophytes and dinoflagellates, especially *Ochromonas caroliniana* and *Gymnodinium* spp. in late spring, but several diatoms, *Nitzchia longissima* and *Cyclotella* sp., were also present at low tide.

During late spring, diatoms were the abundant taxonomic group in Futch Creek. Common diatoms included *Navicula* sp., *Chaetoceros atlanticum*, and *Cyclotella* sp. There were also a small number of dinoflagellates in the upper reaches of Futch Creek during late summer, mostly *Gymnodinium* spp.

Phytoplankton assemblages were more diverse during late summer, especially in Hewletts Creek. Lower Hewletts Creek reaches were dominated by diatoms, *Nitzchia longissima*, *Navicula* sp., *Cyclotella* sp., and *Thalassiothrix frauenfeldii* at high tide. At low tide there were more taxa present in lower creek reaches, including *Gymnodinium* spp, cryptomonads, especially *Cryptomonas* sp., and a very small number of the prasinophyte *Tetraselmis gracilis*. Oligohaline reaches in Hewletts Creek were dominated by chrysophytes and dinoflagellates, mostly *Ochromonas caroliniana*, and *Gymnodinium* spp. The mesohaline reaches of Hewletts Creek during late summer were characterized by *Ochromonas caroliniana*, *Navicula* sp. and *Nitzchia longissima*. Low tide mesohaline reaches were dominated by *Cryptomonas* sp. and *Gymnodinium* spp.

Diatoms were abundant during late summer throughout Futch Creek. Dominant diatom species included *Navicula* sp., *Cyclotella* sp., *Asterionella glacialis*, *Nitzchia longissima*, *Skeletonema costatum*, and *Thalassiothrix frauenfeldii*. There were also a small number of dinoflagellates mainly, *Gymnodinium* spp., present in the upper reaches of Futch Creek.

Correlation Analysis

Pair-wise correlation analyses were utilized to look for significant relationships between productivity, biomass and 10 physical – chemical parameters. A correlation matrix is presented for Futch Creek and Hewletts Creek at high tide and low tide in Tables 7 – 10.

Table 7. Results of correlation analysis for Futch Creek high tide data reported as Pearson correlation coefficients (r)/ probability (p). Shaded areas represent significance with $p<0.05$.

	Temp	Sal	LTurb	LLight	Daily Irr	Sample Irr	LNH_4	LNO_x	LPO_4	LChla	LProd
Temp	1.00										
Sal	-0.1831 0.2850	1.00									
LTurb	0.6771 0.0001	-0.4497 0.0059	1.00								
LLight Atten	0.6289 0.0001	-0.6765 0.0010	0.5498 0.0005	1.00							
Daily Irr	0.3609 0.0306	0.1133 0.5107	0.2496 0.1420	-0.0094 0.9566	1.00						
Sample Irr	-0.1601 0.3508	0.2106 0.2175	-0.0457 0.7915	-0.3542 0.0341	0.6157 <0.0001	1.00					
LNH_4	0.6001 0.0001	-0.4061 0.0140	0.4901 0.0024	0.5178 0.0012	-0.0827 0.6314	-0.3968 0.0166	1.00				
LNO_x	0.2053 0.2297	-0.8173 0.0001	0.5396 0.0007	0.4850 0.0027	-0.0186 0.9144	-0.0024 0.9887	0.4161 0.0116	1.00			
LPO_4	0.4782 0.0032	-0.6563 0.0001	0.6558 0.0001	0.4284 0.0091	0.0235 0.8920	-0.2097 0.2197	0.6981 0.0001	0.7193 0.0001	1.00		
LChla	0.6972 0.0001	-0.3842 0.0207	0.5786 0.0002	0.6031 0.0001	0.1059 0.5389	-0.0068 0.9688	0.5476 0.0068	0.4758 0.0034	0.5369 0.0007	1.00	
LProd	0.8992 0.0001	-0.1528 0.3735	0.6669 0.0001	0.4919 0.0023	0.2301 0.1769	-0.1945 0.2557	0.5546 0.0033	0.3261 0.0523	0.5749 0.0002	0.7103 0.0001	1.00
LRain 24	0.4626 0.0045	-0.0521 0.7629	0.2112 0.2162	0.4216 0.0104	0.1695 0.3229	-0.0297 0.8637	0.2738 0.1061	0.0666 0.6994	0.0798 0.6436	0.6195 0.0001	-0.0470 0.8181
LRain 72	0.5113 0.0014	-0.5210 0.0011	0.3565 0.0328	0.8058 0.0001	-0.1581 0.3570	-0.4243 0.0099	0.5511 0.0005	0.2502 0.1411	0.3533 0.0345	0.5717 0.0003	0.2371 0.2435

Temp = temperature, Sal = salinity, LTurb = Log turbidity, LLight = Log light attenuation, Daily Irr = Total Daily Solar Irradiance, Sample Irr = Solar Irradiance during time of sample incubation, LNH_4 = Log ammonium, LNO_X = Log nitrate, LPO_4 = Log orthophosphate, LChla = Log chlorophyll *a*, LProd = Log Daily Productivity, LRain 24= Log cumulative rainfall 24 prior to sampling, LRain 72 = Log cumulative rainfall 72 hours prior to sampling

Table 8. Results of correlation analysis for Hewletts Creek high tide data reported as Pearson correlation coefficients (r)/ probability (p). Shaded areas represent significance with $p<0.05$.

	Temp	Sal	LTurb	LLight Atten	Daily Irr	Sample Irr	LNH_4	LNO_x	LPO_4	LChla	LProd
Temp	1.00										
Sal	0.0467 0.7868	1.00									
LTurb	0.4164 0.0115	-0.5318 0.0008	1.00								
LLight Atten	0.2585 0.1398	-0.7735 0.0001	0.5172 0.0017	1.00							
Daily Irr	0.3754 0.0241	-0.1443 0.4010	0.2101 0.2187	0.0811 0.6485	1.00						
Sample Irr	0.2911 0.0850	-0.1123 0.5144	0.1574 0.3593	0.0541 0.7611	0.9141 <0.0001	1.00					
LNH_4	0.3904 0.0186	-0.4552 0.0053	0.3228 0.0548	0.5867 0.0003	-0.0319 0.8534	-0.0891 0.6053	1.00				
LNO_x	-0.0046 0.9788	-0.8405 0.0001	0.3708 0.0260	0.6670 0.0001	-0.0243 0.8879	-0.0350 0.8392	0.4529 0.0055	1.00			
LPO_4	0.5028 0.0018	-0.6330 0.0001	0.5745 0.0002	0.7328 0.0001	0.0950 0.5818	0.0960 0.5776	0.7336 0.0001	0.7182 0.0001	1.00		
LChla	0.4643 0.0043	-0.4522 0.0056	0.5655 0.0003	0.2682 0.1251	0.4574 0.0050	0.3114 0.0645	0.1746 0.3084	0.3563 0.0329	0.4664 0.0041	1.00	
LProd	0.6599 0.0001	-0.3015 0.0740	0.6223 0.0001	0.1994 0.2583	0.6032 <0.0001	0.4954 0.0021	0.1486 0.3871	0.2060 0.2282	0.4367 0.0078	0.8306 0.0001	1.00
LRain 24	0.1140 0.5082	-0.0877 0.6109	0.1443 0.4012	-0.1088 0.5402	-0.0488 0.7774	-0.1944 0.2560	-0.0616 0.7211	-0.0927 0.5625	-0.0927 0.5907	0.2232 0.1907	0.1596 0.3524
LRain 72	0.2931 0.0827	-0.0755 0.6616	0.1876 0.2734	0.3475 0.0440	-0.4288 0.0092	-0.4035 0.0147	0.3057 0.0699	0.1508 0.3801	0.3604 0.0308	-0.0496 0.7741	-0.0529 0.7592

Temp = temperature, Sal = salinity, LTurb = Log turbidity, LLight = Log light attenuation, Daily Irr = Total Daily Solar Irradiance, Sample Irr = Solar Irradiance during time of sample incubation, LNH_4 = Log ammonium, LNO_X = Log nitrate, LPO_4 = Log orthophosphate, LChla = Log chlorophyll *a*, LProd = Log Daily Productivity, LRain 24= Log cumulative rainfall 24 prior to sampling, LRain 72 = Log cumulative rainfall 72 hours prior to sampling

Table 9. Results of correlation analysis for Futch Creek low tide data reported as Pearson correlation coefficients (r)/ probability (p). Shaded areas represent significance with $p<0.05$.

	Temp	Sal	LTurb	Daily Irr	Sample Irr	LNH_4	LNO_x	LPO_4	LChla	LProd
Temp	1.00									
Sal	0.3072 0.2471	1.00								
LTurb	0.7194 0.0017	-0.3153 0.2343	1.00							
Daily Irr	-0.1240 0.6727	0.5724 0.0324	-0.3452 0.2266	1.00						
Sample Irr	-0.4559 0.1013	0.2037 0.4850	-0.3843 0.1749	0.7077 0.0046	1.00					
LNH_4	0.6408 0.0075	-0.2363 0.3781	0.6957 0.0028	-0.6944 0.0059	-0.7987 0.0066	1.00				
LNO_x	-0.1348 0.6186	-0.8730 0.0001	0.3010 0.2573	-0.6427 0.0132	-0.5281 0.0522	0.4155 0.1095	1.00			
LPO_4	0.1697 0.5297	-0.8272 0.0001	0.7070 0.0022	-0.4076 0.1480	-0.2554 0.3782	0.5062 0.0454	0.7258 0.0015	1.00		
LChla	0.2399 0.3709	-0.4426 0.0860	0.3602 0.1706	-0.1378 0.6386	-0.3298 0.2495	0.2126 0.4293	0.4944 0.0516	0.4164 0.1086	1.00	
LProd	0.6685 0.0046	0.1813 0.5015	0.3720 0.1560	-0.0922 0.7540	-0.4274 0.1274	0.4009 0.1238	0.5078 0.8316	-0.0256 0.9249	0.5911 0.0159	1.00
LRain 24	0.1044 0.7004	-0.5959 0.0149	0.6395 0.0076	-0.1359 0.6431	0.1298 0.6582	0.3370 0.2018	0.3614 0.1540	0.7664 0.0005	0.2883 0.2789	0.0531 0.8450
LRain 72	0.4297 0.0967	-0.4913 0.0533	0.7738 0.0004	-0.6537 0.0112	-0.3464 0.2250	0.7336 0.0012	0.3983 0.1133	0.7011 0.0025	0.3132 0.2376	0.2860 0.2828

Temp = temperature, Sal = salinity, LTurb = Log turbidity, Daily Irr = Total Daily Solar Irradiance, Sample Irr = Solar Irradiance during time of sample incubation, LNH_4 = Log ammonium, LNO_X = Log nitrate, LPO_4 = Log orthophosphate, LChla = Log chlorophyll *a*, LProd = Log Daily Productivity, LRain 24= Log cumulative rainfall 24 prior to sampling, LRain 72 = Log cumulative rainfall 72 hours prior to sampling

Table 10. Results of correlation analysis for Hewletts Creek low tide data reported as Pearson correlation coefficients (r)/ probability (p). Shaded areas represent significance with p<0.05.

	Temp	**Sal**	**LTurb**	**Daily Irr**	**Sample Irr**	**LNH_4**	**LNO_x**	**LPO_4**	**LChla**	**LProd**
Temp	1.00									
Sal	0.3318 0.2465	1.00								
LTurb	0.5509 0.0412	-0.4566 0.1007	1.00							
Daily Irr	-0.3065 0.3085	0.0402 0.8964	-0.4147 0.1588	1.00						
Sample Irr	-0.3234 0.2812	0.1073 0.7272	-0.4053 0.1695	0.9047 <0.0001	1.00					
LNH_4	0.2897 0.3150	-0.2483 0.3920	0.4308 0.1241	-0.6164 0.0248	-0.5188 0.0693	1.00				
LNO_x	0.0311 0.9197	-0.3349 0.2633	0.3877 0.1906	-0.6776 0.0109	-0.5751 0.0397	0.6974 0.0081	1.00			
LPO_4	0.4264 0.1462	-0.4375 0.1350	0.6973 0.0081	-0.2395 0.4306	-0.1285 0.6756	0.7394 0.0039	0.4509 0.1220	1.00		
LChla	-0.0714 0.8085	-0.6785 0.0076	0.2983 0.3003	0.2960 0.3261	0.1076 0.7264	-0.0493 0.8670	-0.2902 0.3361	0.2841 0.3469	1.00	
LProd	0.0158 0.9592	-0.4823 0.0807	0.3599 0.2062	0.3692 0.2144	0.0700 0.8202	-0.2822 0.3283	-0.2330 0.4436	-0.1629 0.5949	0.6786 0.0076	1.00
LRain 24	0.1254 0.6693	-0.2984 0.3000	0.4567 0.1007	-0.0680 0.8254	0.0493 0.8783	-0.0176 0.9525	0.3608 0.2258	0.2164 0.4775	-0.2183 0.4533	-0.0242 0.9346
LRain 72	0.4055 0.1503	-0.1846 0.5276	0.6186 0.0183	-0.5887 0.0343	-0.4859 0.0923	0.5439 0.0444	0.8300 0.0004	0.5948 0.0320	-0.2845 0.3243	-0.1706 0.5599

Temp = temperature, Sal = salinity, LTurb = Log turbidity, Daily Irr = Total Daily Solar Irradiance, Sample Irr = Solar Irradiance during time of sample incubation, LNH_4 = Log ammonium, LNO_X = Log nitrate, LPO_4 = Log orthophosphate, LChla = Log chlorophyll *a*, LProd = Log Daily Productivity, LRain 24= Log cumulative rainfall 24 prior to sampling, LRain 72 = Log cumulative rainfall 72 hours prior to sampling

There were numerous significant relationships between primary productivity and environmental variables when the data set was analyzed in entirety, all sites, seasons and tides included (Table 11). Phytoplankton productivity displayed significant positive relationships with phytoplankton biomass ($r=0.8275$, $p<0.0001$) and with the physical parameters temperature ($r=0.7541$, $p<0.0001$), turbidity ($r=0.6562$, $p<0.0001$), solar irradiance ($r=0.4551$, $p<0.0001$) and water column light attenuation ($r=0.3763$, $p=0.0003$). Phytoplankton production was also positively correlated with the nutrients orthophosphate ($r=0.4346$, $p<0.0001$) and ammonium ($r=0.3419$, $p=0.0005$). There was a weak negative relationship between productivity and salinity ($r= -0.2854$, $p=0.0042$).

Other noteworthy relationships existed between turbidity and nutrient concentrations; ammonium ($r=0.4645$, $p<0.0001$), nitrate ($r=0.4161$, $p<0.0001$), and orthophosphate ($r=0.6076$, $p<0.0001$; Table 11). There was a weak negative relationship between collective rainfall 72 hours prior to sampling and salinity ($r= -0.3188$, $p=0.0013$). Collective rainfall 72 hours prior to sampling was positively correlated with all nutrient parameters; ammonium ($r=0.4267$, $p<0.0001$), nitrate ($r=0.2907$, $p=0.0035$) and orthophosphate ($r=0.3912$, $p<0.0001$).

Principal Components Analysis

The data set consisted of a large number of interrelated variables (Tables 7 – 11); therefore correlation analysis alone was not a suitable statistical choice.

Table 11. Results of correlation analysis for entire data set, both creeks and both tidal stages, reported as Pearson correlation coefficients (r)/ probability (p). Shaded areas represent significance with p<0.05.

	Temp	**Sal**	**LTurb**	**LLight Atten**	**Daily Irr**	**Sample Irr**	**LNH_4**	**LNO_x**	**LPO_4**	**LChla**	**LProd**
Temp	1.00										
Sal	-0.0682 0.5024	1.00									
LTurb	0.6149 <0.0001	-0.4734 <0.0001	1.00								
LLight Atten	0.4195 <0.0001	-0.7251 <0.0001	0.5554 <0.0001	1.00							
Daily Irr	0.36115 0.0002	0.0455 0.6545	0.1924 0.0564	0.0167 0.8778	1.00						
Sample Irr	0.0273 0.7889	0.0610 0.5484	-0.0239 0.8147	-0.1414 0.1915	0.7758 <0.0001	1.00					
LNH_4	0.4823 <0.0001	-0.4127 <0.0001	0.4645 <0.0001	0.5654 <0.0001	-0.1256 0.2155	-0.3217 0.0012	1.00				
LNO_x	0.0748 0.4620	-0.7254 <0.0001	0.4161 <0.0001	0.5929 <0.0001	-0.1599 0.1140	-0.1674 0.0977	0.5086 <0.0001	1.00			
LPO_4	0.4642 <0.0001	-0.6346 <0.0001	0.6076 <0.0001	0.6022 0.0001	0.0113 0.9118	-0.0563 0.5799	0.7121 <0.0001	0.6494 <0.0001	1.00		
LChla	0.4929 <0.0001	-0.4693 <0.0001	0.5465 <0.0001	0.4009 0.0001	0.3588 0.0003	0.1575 0.1195	0.2581 0.0099	0.1577 0.1189	0.4298 <0.0001	1.00	
LProd	0.7541 <0.0001	-0.2854 0.0042	0.6562 <0.0001	0.3763 0.0003	0.4551 <0.0001	0.1383 0.1723	0.3419 0.0005	0.1180 0.2448	0.4346 <0.0001	0.8275 <0.0001	1.00
LRain 24	0.2597 0.0094	-0.1851 0.0666	0.3775 0.0001	0.3827 0.0003	0.0905 0.3731	0.0536 0.5979	0.1460 0.1494	0.1536 0.1290	0.1596 0.1146	0.1831 0.0697	0.2098 0.0372
LRain 72	0.3668 0.0002	-0.3188 0.0013	0.3166 0.0014	0.6161 <0.0001	-0.3297 0.0009	-0.3893 <0.0001	0.4276 <0.0001	0.2907 0.0035	0.3912 <0.0001	0.0956 0.3467	0.1232 0.2245

Temp = temperature, Sal = salinity, LTurb = Log turbidity, LLight = Log light attenuation, Daily Irr = Total Daily Solar Irradiance, Sample Irr = Solar Irradiance during time of sample incubation, LNH_4 = Log ammonium, LNO_X = Log nitrate, LPO_4 = Log orthophosphate, LChla = Log chlorophyll *a*, LProd = Log Daily Productivity, LRain 24= Log cumulative rainfall 24 prior to sampling, LRain 72 = Log cumulative rainfall 72 hours prior to sampling

Principal components analysis was utilized to help reduce the dimensionality of the data set. Thirteen physical, chemical and biological variables were utilized in a factor analysis. Factor 1 alone explained 40 percent of the variability in the data set. Factors 1 – 4 together explained 81 percent of the data (Table 12). Therefore, only Factors 1 – 4 were analyzed for the purposes of the present research.

The variables that best fit each factor are listed in Table 13. Factor 1 has the strongest loadings on the physical variables temperature and water column light attenuation (negative) and an intermediate loading on ammonium. Factor 2 has the highest loadings on salinity (negative) and orthophosphate. Factor 3 has the highest loadings on chlorophyll *a* and total solar irradiance during incubation. Factor 4 has an intermediate loading on total rainfall 72 hours prior to sampling. Primary productivity was analyzed for each factor by season, site and tidal stage using scatter plots of observed productivity.

Regression analysis revealed significant relationships between primary productivity and Factor 1 ($p<0.0001$), Factor 2 ($p=0.0073$), Factor 3 ($p=0.0147$) and Factor 4 ($p=0.0047$). The scatter plot in Figure 12 indicates a strong positive trend of higher predicted values of primary productivity with increasing values of Factor 1. Predicted values of primary productivity were also higher with increasing values of Factor 2 (Figure 13). Factors 1 and 2 together represent the mechanistic variables that drive phytoplankton production in local tidal creeks. The results from the PCA suggest that phytoplankton productivity is primarily driven by temperature and water column irradiance and secondarily by nutrient

Table 12. Eigenvalues for the principal components correlation matrix.

Factor Number	Eigenvalue	Cumulative Percentage
1	4.9183	0.4099
2	2.3921	0.6092
3	1.3586	0.7224
4	1.0528	0.8102
5	0.7450	0.8722
6	0.4918	0.9132
7	0.2907	0.9375
8	0.2434	0.9577
9	0.2104	0.9753
10	0.1246	0.9857
11	0.1064	0.9945
12	0.0656	1.0000

Table 13. Rotated factor pattern for principal components analysis.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Temperature	**0.9204**	-0.0248	0.1155	0.2243
Salinity	0.0358	**- 0.9015**	-0.0386	-0.2720
Turbidity	0.6099	0.3888	0.0949	0.4758
Light Attenuation	**- 0.9260**	-0.1730	-0.1024	0.0334
Total Daily Solar Irradiance	0.3589	0.6454	-0.0697	0.4587
Irradiance During Incubation	0.3674	-0.0618	**0.8808**	0.0343
Chlorophyll *a*	-0.0153	-0.0162	**0.9557**	-0.0576
Ammonium	**0.7906**	0.1082	0.2651	0.2609
Nitrate	0.5661	0.5497	-0.2484	-0.0364
Orthophosphate	0.0508	**0.9151**	-0.0258	0.1042
Rain 24hrs	0.4220	0.6176	-0.0309	-0.3528
Rain 72hrs	0.1742	0.1480	-0.0392	**0.7870**

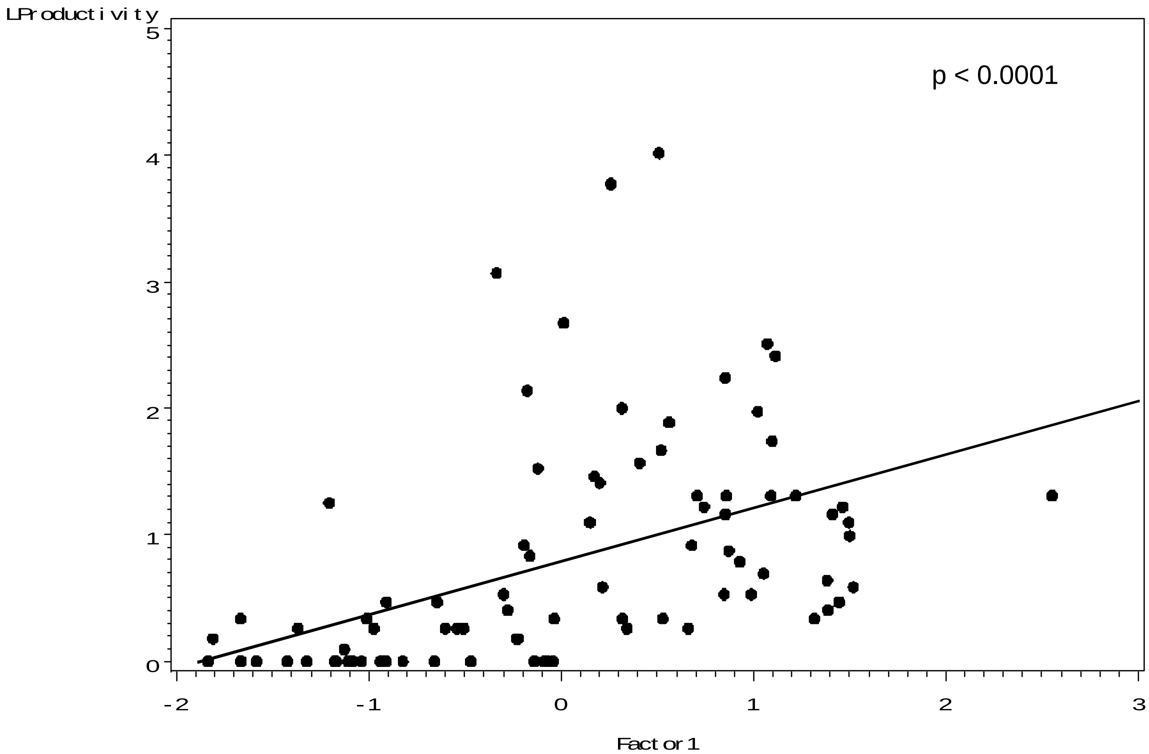


Figure 12. Scatter plot of measured values of phytoplankton primary productivity and Factor 1.

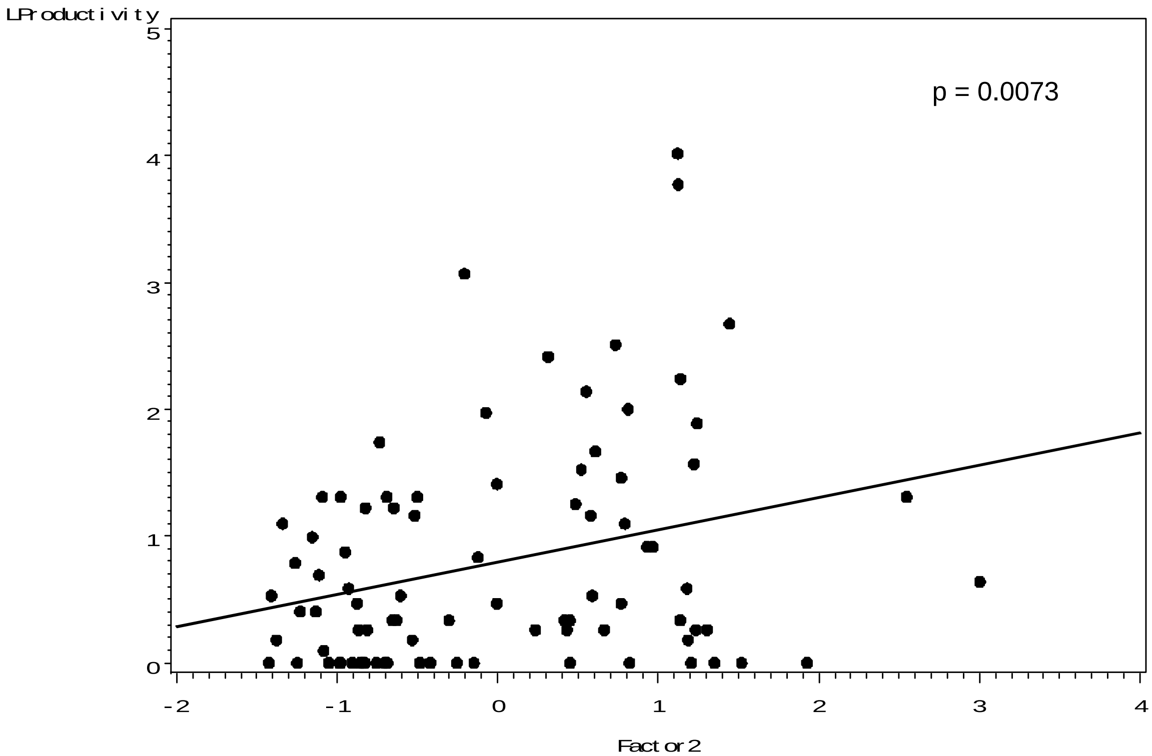


Figure 13. Scatter plot of measured values of phytoplankton primary productivity and Factor 2.

supply, mostly ammonium and orthophosphate. Results from the PCA categorized ammonium and orthophosphate in two separate factors, suggesting two different sources of nutrient supply. Ammonium separated into Factor 1 and displayed a distinct seasonal trend, suggesting the importance of *in situ* recycling, especially during summer months when biological processing is high in tidal creeks. Orthophosphate, however, separated into Factor 2 with salinity suggesting this nutrient is introduced into tidal creeks via non-point source runoff from the upland watershed.

There was a positive trend of higher predicted values of primary productivity with increasing values of Factor 3, solar irradiance and biomass (Figure 14). Primary productivity values are higher during summer when phytoplankton biomass is high and there is more solar irradiance available for phytoplankton growth during the incubation period.

Factor 4 most strongly represents the flushing effect from meteorological events. Predicted values of primary productivity increased with increasing values of Factor 4 (Figure 15), suggesting that non-point source runoff from the upland watershed does enhance primary production, but has a delayed effect, in this case up to 72 hours after a rain event.

Regression Analysis

A separate regression analysis was run for the entire data set, independent of the PCA regression analysis. The purpose of this analysis was to determine which variables or combinations of variables are the most

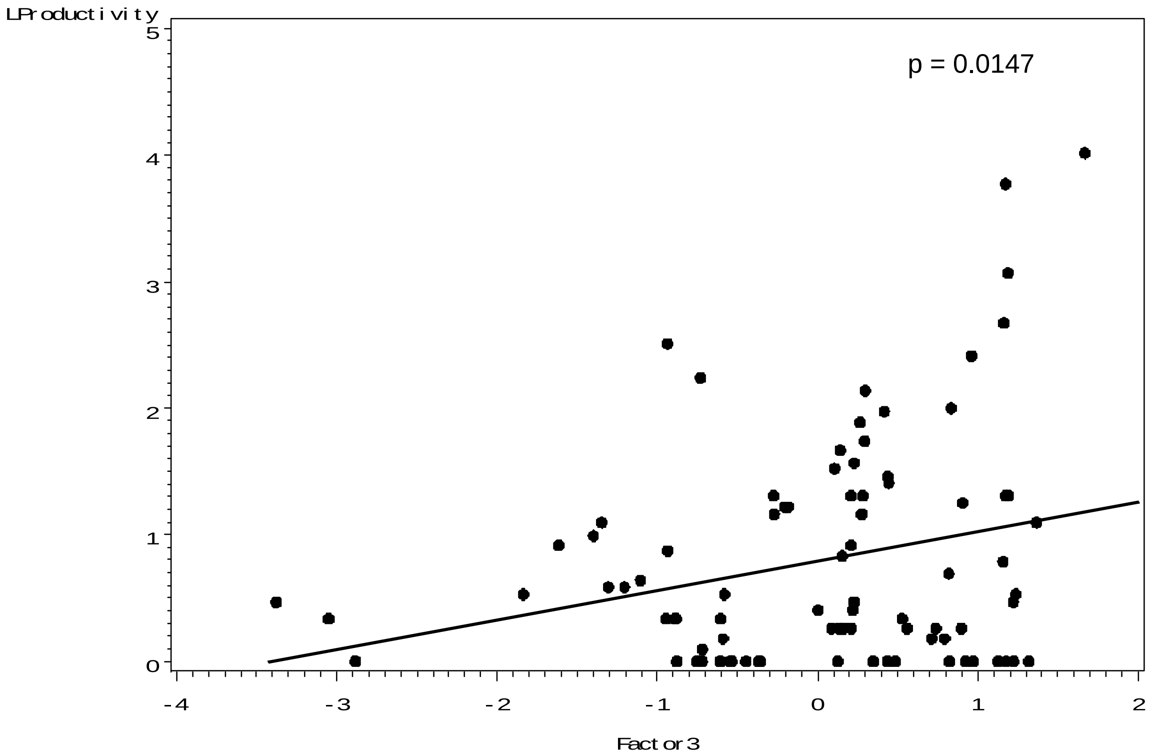


Figure 14. Scatter plot of measured values of phytoplankton primary productivity and Factor 3.

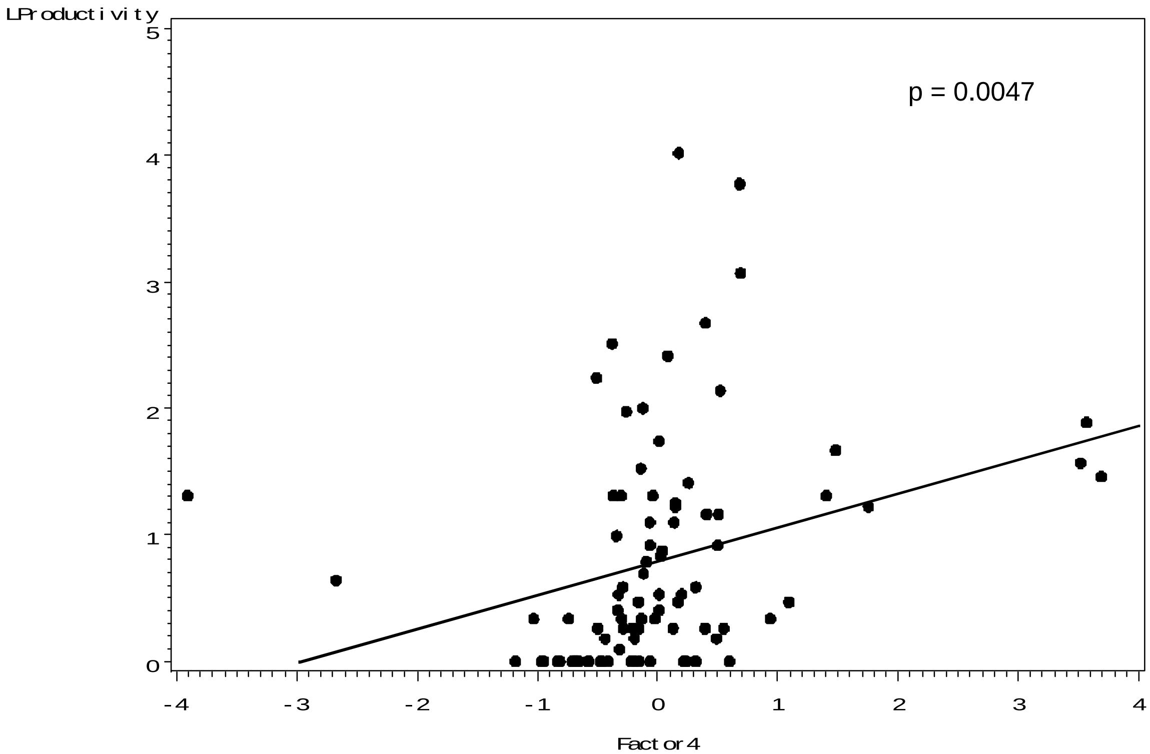


Figure 15. Scatter plot of measured values of phytoplankton primary productivity and Factor 4.

instantaneous predictors of phytoplankton productivity. It is important for management practices that scientists can quickly predict primary productivity and not have to wait for the delayed and sometimes expensive results of chemical assays. A number of independent variables were tested against one dependent variable, phytoplankton primary productivity (Table 14). The most instantaneous and economical predictor of phytoplankton production is a combination of temperature and chlorophyll *a* [log phytoplankton productivity (mgC m^{-3} day^{-1}) = 2.04 + 0.12(temperature) + 1.02(log chlorophyll *a*)]. The combination of temperature and chlorophyll *a* explains approximately 83% of the variability in productivity.

DISCUSSION

A number of environmental variables have been shown to play a role in regulating primary productivity by phytoplankton in estuarine systems, including light, temperature, salinity and some function of nutrient availability. This study confirms that considering a single parameter as the driving mechanism of phytoplankton production is not sufficient, especially in dynamic tidal creek ecosystems.

Primary productivity by phytoplankton typically peaks in summer, decreases in fall and winter and then begins to rise again in early spring. Temperature, water column irradiance and nutrient availability act collectively as the major driving forces of phytoplankton production. Increasing temperatures in

Table 14. Results of regression analyses for phytoplankton primary productivity.

Independent Variable(s)	R^2	P-value	F-value
Water temperature	0.5914	<0.0001	123.1
Light Attenuation	0.1416	0.0003	14.0
Chlorophyll *a*	0.6430	<0.0001	153.1
Daily Solar Irradiance	0.2338	<0.0001	25.9
Water temperature Chlorophyll *a*	0.8305	<0.0001 <0.0001	205.8
Water temperature Chlorophyll *a* Light attenuation	0.7344	<0.0001 <0.0001 0.1556	139.6
Daily Solar Irradiance Water temperature	0.6228	0.0099 <0.0001	69.3

spring and summer trigger phytoplankton productivity and biomass. During winter months, phytoplankton are unable to reach maximum potential even though water column irradiance is high and nutrient supply is not always limited, suggesting temperature could be the most controlling factor of phytoplankton productivity. This is consistent with similar studies of southeastern estuaries whereby biological processing, including phytoplankton production and biomass, displayed distinct seasonal trends (Caffrey 2004, Dame et al. 2000, Lewitus et al. 1998, Mallin 1994, Baird and Ulanowicz 1989). It is likely that while temperature is the most important physical factor forcing phytoplankton productivity in these tidal creeks, nutrient availability and water column irradiance are likely secondary, but significant, determinants of productivity.

Futch Creek and Hewletts Creek are both closely linked to a highly urban and suburban landscape and it is rare that nutrient supply of ammonium, nitrate, and orthophosphate is limiting in the upper reaches (Tables 2 and 3). Lower creek reaches, however, have consistently low nitrogen concentrations (Tables 2 and 3). Median inorganic N:P ratios in the upper reaches of Futch and Hewletts Creek were close to the Redfield ratio of 16; 15 at FC-17, 15 at NB-GLR and 16 at SB-PGR. Median N:P ratios in the lower reaches of Futch and Hewletts Creek were 8 at FC-4, 7 at FC-6 and 7 at HC-2 suggesting nitrogen limitation. Previous nutrient addition bioassays have demonstrated nitrogen limitation, as nitrate-nitrogen, in lower creek reaches of both Futch and Hewletts Creek (Mallin et al. 2004). Upper Hewletts Creek has displayed occasional nitrogen limitation and upper Futch Creek has displayed nitrogen limitation with occasional phosphorus limitation, as inorganic phosphorus, in upper Futch Creek. Nearby Howe Creek also displayed occasional nitrogen and phosphorus co-limitation (Mallin et al. 2004). Neighboring waters in the Intracoastal Waterway, however, have displayed some silica (Si) limitation (Cahoon personal communication), and urbanized estuaries in South Carolina have displayed a higher tendency for Fe stress when compared to forested estuaries (Lewitus et al. 2004). While micronutrients such as Fe and Si were not analyzed in the present study, an investigation of micronutrient concentrations in local creeks could prove useful in future phytoplankton research.

Nutrients, especially ammonium and orthophosphate, tended to be higher during summer months and higher in upper creek reaches. Nutrient concentrations were usually more elevated in Hewletts Creek compared to Futch Creek, although not always significant. Development in the Futch Creek watershed is slightly lower than the Hewletts Creek watershed; however, the likely origin of inorganic nutrient supply in both creeks is nonpoint in origin, e.g., storm water runoff, groundwater, sedimentation, fertilizers and animal waste, especially in the upper reaches. Nitrate nitrogen was the principal dissolved inorganic nutrient compound in both Futch and Hewletts Creek. Nitrate concentrations draining from two golf courses located in the upper Hewletts Creek watershed average about 0.32 mg l^{-1} (Mallin and Wheeler 2000). The upper reaches of Futch Creek receive nitrate nutrient additions from upslope golf courses through groundwater springs (Roberts 2002). Both watersheds have single family homes along creek banks and are therefore also subject to nutrient additions from residential fertilizer application to lawns and gardens as well as domestic animal wastes. Futch Creek has been previously determined to have high flushing properties, approximately 0.4 - 0.5 days (Hales 2001), which could act to buffer some of the effects of eutrophication.

While nonpoint source runoff does play a large role in nutrient loading to Futch and Hewletts Creek, increased biological processing during summer months could favor *in situ* regeneration of ammonium. Although there is still little data concerning nutrient regeneration rates in North Carolina tidal creeks, studies demonstrate increased ammonium concentrations directly downstream of transplanted oyster reefs (Nelson et al. 2004). Ammonium generation from nekton excretion in tidal creeks in South Carolina was 6-12 times higher in the summer (Haertel-Borer et al. 2004). Regenerated nutrients, like NH_4, are the major nitrogen sources supporting phototrophic growth in some South Carolina tidal creeks and hypothesized sources stem from microzooplankton and oysters (Wetz et al. 2002). Nutrient regeneration proves especially important to phytoplankton assemblages in the lower reaches of tidal creeks since upper creek assemblages utilize much of the anthropogenically introduced sources of dissolved inorganic nitrogen.

Phosphate concentrations in these tidal creeks as well as other southeastern estuaries have displayed seasonal trends similar to ammonium (Mallin et al. 1999b). However, the apparent source of phosphate is more terrestrial in nature as suggested by the results of PCA. It is likely that seasonal trends are a function of low dissolved oxygen conditions prevalent during summer months, allowing sediment – bound phosphate to enter the water column (Mallin et al. 1999b).

Heavy rainfall following storm events appears to be a source of new nutrients into tidal creeks as evidenced by elevated nutrient concentrations following rain events. Allochthonous sources of materials, including orthophosphate, ammonium, nitrate and silica, are introduced into tidal creeks from both the upland watershed as well as surrounding marsh surfaces during heavy rain events, enhancing primary productivity (Hubertz and Cahoon 1999, Mallin et al. 1993). However, there was an apparent delayed effect from rainfall and resultant runoff, in this case approximately 72 hours. Shallow tidal creeks in South Carolina have displayed a lack of persistent freshwater inputs. Strong ecological linkages to upland runoff during rain events are short-lived, suggesting a more self-regulating system (White et al. 2004). This is contrary to the findings of current and previous research. Pulses of freshwater runoff from the upland watershed in local tidal creeks act to reduce tidal exchange rates and favor pollutant retention (Hales 2001). Disturbance associated with rain events in both creeks appears to be more long-lived than South Carolina tidal creeks as evidenced by decreased salinities following heavy rain in both creeks for up to one week in some instances. Therefore, it is likely that these systems are not always self-regulating and nonpoint source runoff may be an overriding factor in ecosystem processing.

Light can be limiting to phytoplankton production in estuaries due to their turbid nature. It has been suggested that light may be a more influential factor than nutrient supply in terms of microalgal production in shallow, turbid, salt marsh estuaries of Georgia, North Carolina and South Carolina (Dame et al. 2000, Mallin 1994). The intensity and amount of light available to phytoplankton can be altered by both solar irradiance and water column irradiance over long- and short-term time scales. Long-term light availability is influenced by the diurnal path of the sun, season and meteorological conditions. Short-term light availability is regulated by internal tide, wind and current induced motions, surface waves and cellular motility. Data from the present study indicate that while long-term light availability is important (Figure 14), short-term variability in light attenuation plays a more significant role in regulating phytoplankton productivity. Light attenuation values were highest seasonally during summer months and following major stochastic events, suggesting the potential for light limitation. Due to tide and current induced motions within shallow tidal creeks phytoplankton cells are likely well mixed through the light-limited zones.

Major stochastic events, such as Hurricane Charley, can have a pronounced effect on ecosystem processes. Phytoplankton productivity was depressed in August, after Hurricane Charley, when productivity would usually be elevated. Hurricane Charley brought with it over 3 inches of rain. High flushing from freshwater runoff of the upland watershed following rain events has been shown to exert a strong influence on the spatial and temporal distribution of phytoplankton in some estuaries (Therriault et al. 1990). Phytoplankton abundance can be physically restricted upstream due to increased flushing velocities. A previous study of flushing rates in southeastern North Carolina estuaries indicates that continuous fresh water input decreases water residence time in local tidal creeks (Hales 2001). While smaller pulses of rain have proven to increase pollutant retention and reduce flushing, the continuous and severe rains following Hurricane Charley most likely flushed out much of the algal biomass in these tidal creeks, replacing it with a high biochemical oxygen demand (BOD) organic load, which eventually led to the water column hypoxia that was present in Hewletts Creek two weeks after the hurricane. Remaining phytoplankton biomass, mostly centric and pennate diatoms, were likely limited by decreased water column irradiance.

Peaks in primary productivity coincided with the summer chlorophyll *a* maxima in both creeks. Phytoplankton biomass was thus controlled primarily by temperature-driven patterns, a trend displayed in numerous southeastern estuaries (White et al. 2004, Dame et al. 2000, Lewitus et al. 1998, Mallin 1994). Phytoplankton peaks in Hewletts Creek were characteristically higher than Futch Creek, reiterating developmental impacts and arguing for eutrophication.

The average phytoplankton assimilation rates, or biomass specific primary productivity, found in local tidal creeks are considerably higher than rates in nutrient-depleted zones (1-3 mgC (mg chl $a)^{-1}$ hr^{-1}), but only slightly higher than rates of nutrient-rich coastal upwellings (10-15 mgC (mg chl $a)^{-1}$ hr^{-1}; Fisher et al. 1982). The assimilation number is often a function of temperature (Pinckney et al. 1997, Fisher et al. 1982). Average assimilation rates in Hewletts Creek were four times higher as temperatures increased from 10 to 27°C and rates in Futch Creek were nearly seven times higher as temperatures increased from 8 to 27°C.

In order for phytoplankton to achieve maximum photosynthesis, temperature, nutrients and other factors must be such that cells are growing rapidly (Harris et al. 1980). Carbon assimilation rates were lower in the upper reaches of Hewletts Creek compared to lower reaches, which could suggest a decrease in photosynthetic efficiency as a result of physical limitation. This is contrary to larger North Carolina estuaries, such as the Neuse River Estuary, in which highest assimilation rates occurred in the middle reaches of the estuary and the lowest values were reported in the lower reaches (Pinckney et al. 1997). The spatial variability in carbon assimilation rates could be attributed to a number of factors, including both physical and chemical limitations. Harris et al. (1980) demonstrated that rapid and continued mixing in some lake environments may lead to decreased nutrient uptake in phytoplankton, thereby suppressing photosynthetic efficiency. This phenomenon was more severe during warm months than cold months (Harris et al. 1980). Increased assimilation rates in the lower reaches compared to upper creek reaches could also be periodically attributed to light penetration. While lower creek reaches are not generally light limited, upper reaches will periodically display seasonal light limitation. When phytoplankton cells are subject to a light – saturated environment, photosynthetic efficiency is high. Decreases in photosynthetic efficiency per unit chlorophyll have been documented in marine phytoplankton under light – limited conditions (Perry et al. 1981) as well as in shade adapted phytoplankton (Falkowski 1981), suggesting some phytoplankton are unable to attain optimal photosynthesis in light – limited environments.

Resident phytoplankton taxa may also be an important determinant of assimilation rate. For example, when larger diatoms are numerically dominant biomass data will reflect the importance of these larger cells. However, when smaller phytoflagellates dominate numerically, biomass might remain low even though cell densities are high. Diatoms were not found in the oligohaline reaches of Hewletts Creek during late spring and summer, possibly attributed to salinity characteristics of the upper reaches. While diatoms can be abundant in high salinity areas of estuaries, similar studies of the Cape Fear River Estuary (Carpenter 1971) and the upper Chesapeake Bay (Marshall 1966) report a decrease in the relative importance of diatoms with decreasing salinity (Stanley and Daniel 1985). The lack of larger diatoms and increasing importance of phytoflagellates in the upper oligohaline reaches of Hewletts Creek could suggest that while there were abundant smaller microalgae photosynthesizing, their relative importance may have been misrepresented in the biomass data, therefore resulting in lower assimilation rates.

This study demonstrates that phytoplankton primary production in Futch Creek and Hewletts Creek is high, equal to or greater than that of larger eutrophic estuaries such as the Neuse and Pamlico River Estuaries (Table 15). However, local tidal creeks have not suffered from problems traditionally associated with eutrophication. Chronic algal blooms, toxic blooms and large fish kills have not been recorded in these systems, which leads to an important question. What proportion of phytoplankton primary production is removed through natural mortality, grazing, current or sedimentation? When investigating

Table 15. Annual primary production by phytoplankton in Futch Creek and Hewletts Creek as compared to rates in other coastal NC systems, expanded from Mallin 1994.

Beaufort Estuaries	56 gC m^{-3}
Neuse River Estuary	75 gC m^{-3}
Futch Creek	91 gC m^{-3}
South River	144 gC m^{-3}
Pamlico River Estuary	150 gC m^{-3}
Hewletts Creek	246 gC m^{-3}

energy transfer from primary production by phytoplankton to higher trophic levels, it is important to consider the fate of phytoplankton primary production in tidal creek ecosystems. A large portion of energy transfer in mesotrophic and eutrophic systems is thought to follow the traditional food chain of phytoplankton – zooplankton – fish (Fenchel 1988). However, it has been suggested that many estuarine systems are highly complex in terms of sources of primary production and consequential trophic connections (Schoener 1989). Although rates of energy transfer by phytoplankton primary production have been well documented in larger estuaries, this has yet to be experimentally quantified in local tidal creeks.

While the effects of top predatory fish on phytoplankton abundances may be limited (Posey et al. 1995), consumption by intermediate trophic levels can have a significant effect on phytoplankton. As previously stated, upper creek reaches of both creeks are characterized by muddy channels and lower reaches consist of sandy sediments and scattered oyster reefs. Models of bivalve filtration rates in shallow waters predict that sufficient numbers of bivalves can control phytoplankton biomass, as evidenced in the present research by the decrease in chlorophyll *a* spatially from upper reaches to lower reaches. A previous studies of bivalve populations in Hewletts Creek demonstrated 10-25% decreases in chlorophyll *a* concentrations as water flowed over oyster reefs, especially during summer months when phytoplankton biomass was high (Cressman et al. 2003). Wetz et al. (2002) found significantly lower numbers of phototrophic flagellates and some diatoms in creeks with oysters reefs as compared to creeks without oyster reefs.

Zooplankton community grazing rates have shown a positive correlation with primary productivity and phytoplankton abundance in the Neuse River Estuary (Mallin and Paerl 1994), and studies on the Chesapeake Bay demonstrate seasonal trends whereby zooplankton grazing of phytoplankton is greatly reduced due to top-down control by ctenophores and sea nettles (Baird and Ulanowicz 1989). In the pristine North Inlet in coastal South Carolina, microzooplankton grazing, rather than nutrients, limited phytoplankton during summer months (Lewitus et al. 1998). If the system is dominated by easily grazed and assimilated planktonic species, trophic efficiency should be high. Diatoms are generally good food sources for zooplankton, larval fish and other benthic invertebrates. Cryptomonads and dinoflagellates, with a few toxic exceptions, are also a valuable food source, and there is literature noting zooplankton grazing preference for dinoflagellates (Mallin and Paerl 1994). A cryptomonad bloom in Hewletts Creek in 1999 led to enhanced grazing by nontoxic *Pfiesteria* spp. zoospores (Mallin et al. 2004). Cyanobacteria can often be toxic and inedible (Paerl et al. 2003, Mallin and Paerl 1994). Diatoms, dinoflagellates, chrysophytes and cryptophytes were the dominant functional groups present during spring and summer of 2004. Since these groups are all easily assimilated, it is expected that trophic efficiency and grazing should be high and could have an effect on realized phytoplankton productivity.

CONCLUSIONS

Data suggest that the characteristic physical environmental forces (temperature and light) impacting a dynamic tidal creek system govern basic seasonal, temporal and tidal patterns in phytoplankton production. Nutrient supply, however, is an important secondary factor driving phytoplankton production as greater anthropogenic nutrient loading did lead to greater phytoplankton productivity in the more developed watershed. A comparative analysis of annual primary production by phytoplankton in Futch Creek and Hewletts Creek with other neighboring North Carolina estuaries emphasizes their importance as a coastal resource. Salt marsh estuaries provide a nutritional food base for commercially important finfish and shellfish. The moderate to high primary production by phytoplankton demonstrated in this research suggests that local tidal creeks are no exception and need to be properly managed to preserve and restore their integrity as an environmental resource.

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